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Seasonal variability in diversity and species richness of ephemeropteran and plecopteran communities in a boreal stream

JO VEGAR ARNEKLEIV

Arnekleiv, J.V. 1985. Seasonal variability in diversity and species richness of ephemeropteran and plecopteran communities in a boreal stream. *Fauna norv. Ser. B. 32,* 1–6.

Benthic samples were taken with a Surber-sampler from one locality in Trøndelag, Central Norway about twice monthly throughout a year. Ephemeroptera and Plecoptera spp. obtained are listed and dominance determined. Species richness varied seasonally. Both species diversity and evenness were on average higher for the plecopteran community than for the ephemeropteran community. The two groups tended to have their highest species richness and diversity values at different seasons. Ephemeroptera had a peak in both species richness, diversity and evenness in summer while the Plecoptera showed their lowest values in this season. The species diversity in one season was uncorrelated with that in another and was for both Ephemeroptera and Plecoptera dependent upon the relative species abundances (the evenness component) in all seasons. Seasonal variations in diversity are discussed with respect to the species' life cycles. Diversity of ephemeropteran and plecopteran communities varied independent of each other through the year. Differences between the two communities with respect to diversity are discussed.

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INTRODUCTION

Many papers dealing with various aspects of species diversity have accumulated since the early 1960's. However, relatively little attention has been directed towards aquatic invertebrate communities. Recent papers concerning diversity problems in running water environments include Mackay & Kalff (1969), Ulfstrand (1975), Wilhm (1975), Friberg et al. (1977) and Statzner (1981).

Diversity has been used as an index in monitoring changes in stream communities, for example in connection with pollution (Wilhm 1975). The limits of this index value are not clear, and numerous factors have been discussed to explain differences in species diversity between different habitats (Ulfstrand 1975, Friberg et al. 1977). However, the biological meaning of diversity is difficult to estimate, and further studies on animal communities at all seasons seem necessary to evaluate the significance of diversity.

This paper deals with diversity, species richness and evenness in ephemeropteran and plecopteran communities from a single habitat throughout the year. In this study the species composition and life cycle strategies of Ephemeroptera and Plecoptera were known (Arnekleiv 1981) and seasonal changes in diversity could be discussed on this background. Furthermore, the material allows comparison of diversity indexes from the two communities in all seasons.

STUDY AREA, MATERIAL AND METHODS

The study was carried out in the stream Sagelva which drains about 82 km^2 of coniferous forest area in Trøndelag province, Central Norway (63°21'N, 10°38'E). Water temperatures ranged from 18.1°C (4 July 1978) to 0.0°C (winter). The river is ice-covered from about late November to May. During the period of sampling (April 1978–May 1979) the discharge varied from 5 to 3330 l/s. Both temperature and discharge fluctuated rapidly.

The bottom fauna samples were taken where the river flows through mixed forest, about 250 m a.s.l. and 1.3 km from the river mouth. At the sampling site the river is 6–8 m wide and 5–30 cm deep during mean discharge. Water velocity generally varied from 5 to 40 cm/s. The bottom substrate was relatively homogeneous and consisted of stones, 2–10 cm in diameter.

Apart from scattered areas with aquatic mosses, no aquatic vegetation was present.

Sampling was carried out at a single locality about twice monthly throughout a year. Sampling areas were chosen to be as homogeneous as possible with respect to substrate and allochthonous material on the bottom. On each occasion twenty bottom samples were taken in the whole river transect using a Surber sampler (surface area 1500 cm^2) strengthened with a solid metal frame which prevented animals drifting from outside the sampling area into the net bag (mesh size 500 µm). The animals present were sorted and preserved in 80% alcohol.

Species diversity (H') and evenness (J') were calculated according to Peet (1974):

$$H' = -\sum_{n=1}^{S} P_i \ln P_i$$ where P_i is the proportion on the i:th species in the set of S species,

and $$J' = \frac{H'}{H_{max}}$$ where $H_{max} = \ln S$

H' and J' is calculated for each sampling occasion to give «moment diversity» values that can show variation in diversity from time to time. In calculating H' and J' for longer periods («season diversity»), I used average P_i-values resulting from several series in the actual season.

Table 1. Total number and species abundance (%) of Ephemeroptera nymphs for the whole material.

Species	Number	%
Baetis rhodani	6458	54,5
Baetis sp.	1419	12,0
Heptagenia joernensis	1239	10,4
Baetis niger	1005	8,5
Ameletus inopinatus	518	4,3
Baetis muticus	373	3,1
Heptagenia dalecarlica	260	2,2
Centroptilum luteolum	215	1,8
Baetis scambus	206	1,7
Ephemerella aurivillii	81	0,7
Baetis subalpinus	30	0,25
Leptophlebia marginata	18	0,15
Leptophlebiidae	12	0,10
Heptagenia sp.	7	0,06
Paraleptophlebia sp.	6	0,05
Siphlonurus lacustris	4	0,03
Leptophlebia vespertina	2	0,02
Paraleptophlebia cincta	1	0,01
Heptagenia fuscogrisea	1	0,01
Procloeon bifidum	1	0,01
Totalt	11856	~100
Number of species	16	
Number of sampling occasions	25	
Number of samples	461	

RESULTS

Species richness, abundance and dominance

A total of 11800 aphemeropteran nymphs and 7300 plecopteran nymphs were collected during the investigation period. The samples yielded on average more ephemeropteran nymphs than plecopteran nymphs, indicating a higher population density of the former group.

Sixteen species of Ephemeroptera and eighteen species of Plecoptera were recorded during the year (Tables 1 and 2). The most abundant ephemeropteran species was *Baetis rhodani*, (Pictet), which constituted more than 50% of all Ephemeroptera nymphs, and was present throughout the year. Eight species occurred in low numbers, making up less than 1% of total numbers.

Among the Plecoptera, *Capnia atra* Morton was the most abundant species, constituting about 15% of total numbers. *Brachyptera risi* (Morton) and *Leuctra fusca* (L.) were also common, respectively with 13 and 12% of total numbers. All these stonefly species are omnivorous (Brinck 1949) and are widely distributed in Norway (Lillehammer 1974). The predaceous Plecoptera constituted only 17% of the plecopteran fauna, and was dominated by *Diura nanseni* (Kempny).

Species richness varied through the year (Table 3), and in the Ephemeroptera was higher during summer and autumn than during winter and spring. In contrast to that of Ephemeroptera the species richness of Plecoptera showed the highest value during winter and lowest during summer. The number of species at each sampling occasion (20 samples) varied from 4 to 12 species of Ephemeroptera and from 5 to 12 species of Plecoptera.

Table 2. Total number and species abundance (%) of Plecoptera nymphs for the whole material.

Species	Number	%
Capnia atra	1072	14,6
Leuctra sp.	958	13,0
Brachyptera risi	926	12,6
Leuctra fusca	873	11,9
Amphinemura sulcicollis	575	7,8
Siphonoperla burmeisteri	530	7,2
Diura nanseni	497	6,8
Leuctra hippopus	379	5,2
Amphinemura sp.	252	3,4
Capniidae	246	3,3
Taeniopteryx nebulosa	201	2,7
Capnopsis schilleri	195	2,6
Isoperla sp.	126	1,8
Leuctra nigra	65	0,9
Nemoura avicularis	64	0,9
Perlodidae	57	0,8
Nemoura cinerea	56	0,7
Capnia sp.	51	0,7
Leuctra digitata	48	0,6
Isoperla obscura	48	0,6
Amphinemura standfussi	48	0,6
Nemoura sp.	21	0,3
Isoperla grammatica	11	0,1
Plecoptera indet.	8	0,1
Amphinemura borealis	7	0,1
Diura sp.	3	0,04
Capnia pygmaea	1	0,01
Totalt	7318	~100
Number of species	18	
Number of sampling occasions	25	
Number of samples	461	

Table 3. Species richness values for Ephemeroptera (a) and Plecoptera (b) at different seasons. Sx = average number of species, SD = standard deviation, ln S = logaritmic value of number of species.

		Winter	Spring	Summer	Autumn
a)	Sx	6.8	5.7	7.6	7.6
	SD	1.6	1.7	0.8	2.6
	lnS	1.89	1.70	2.01	1.99
b)	Sx	10.8	9.4	5.8	10.0
	SD	0.8	1.8	1.2	0.7
	lnS	2.15	2.15	1.86	2.30

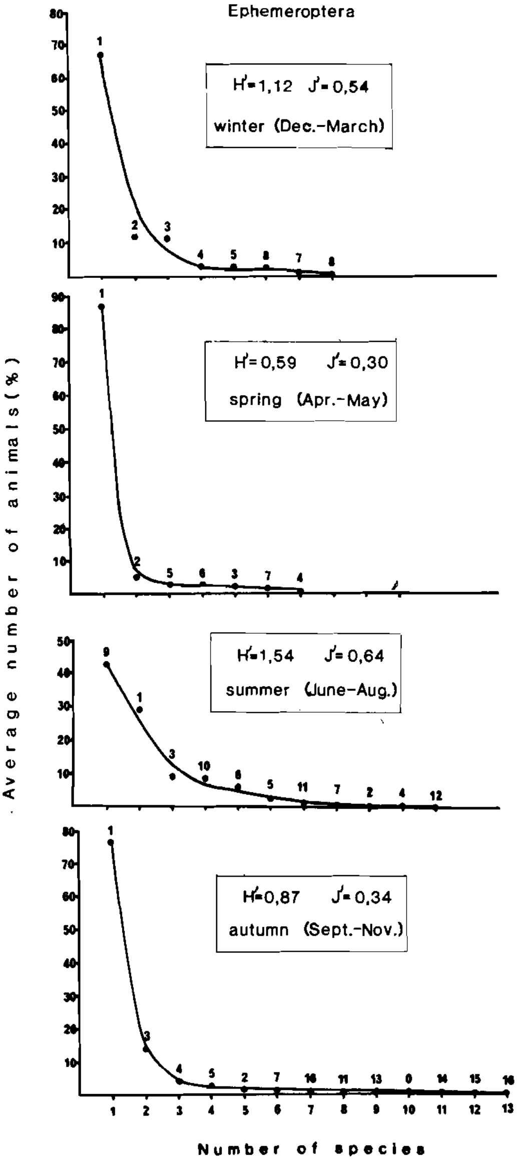

Fig. 1. Comparsion of number of species and average number of individuals among species in Ephemeroptera. H' = Shannon-Weaver index, J' = Evenness index. Numbers by each plot give the identity of the species as follows: 1. *Baetis rhodani*, (Pictet), 2. *Ameletus inopinatus*, Eaton, 3. *B. niger* (L.), 4. *Centroptilum luteolum* (Müller), 5. *Heptagenia dalecarlica*, Bengtsson, 6. *B. muticus* (L.), 7. *Ephemerella aurivillii* (Bengtsson), 8. *Leptophlebia vespertina*, (L.), 9. *H. joernensis*, (Bengtsson), 10. *B. scambus*, Eaton, 11. *B. subalpinus* (Bengtsson), 12. *Siphlonurus lacustris*, Eaton, 13. Paraleptophlebia sp., 14. *Leptophlebia* sp, 15. *H. fuscogrisea* (Retzius), 16. *Procloeon bifidum* (Bengtsson).

Species diversity and its components at different seasons

Species diversity and evenness for the ephemeropteran and plecopteran communities at different seasons are shown in Figs. 1 and 2. Both species diversity and evenness were generally higher for the plecopteran community than for the ephemeropteran community.

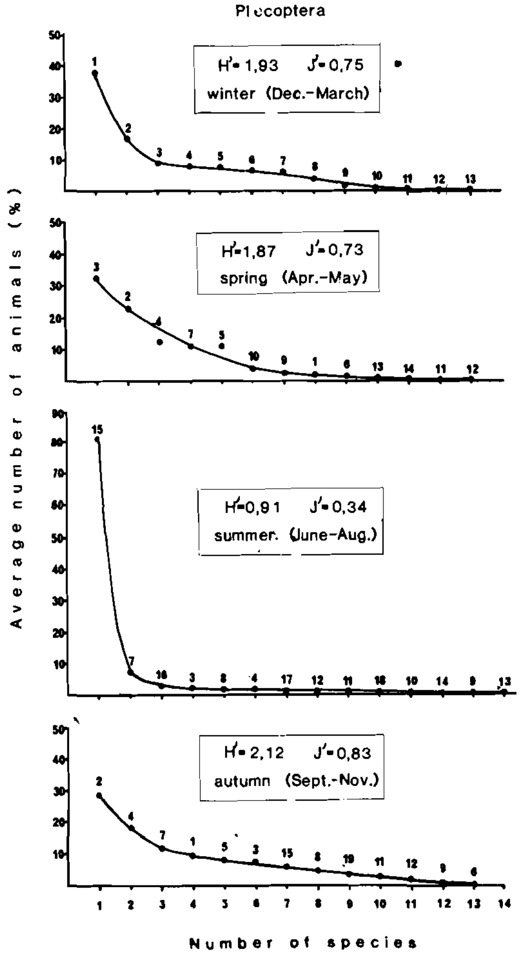

Fig. 2. Comparison of number of species and average number of individuals among species in Plecoptera. H' = Shannon-Weaver index, J' = Evenness index. Numbers by each plot give the identity of the species as follows: 1. *Capnia atra* Morton, 2. *Brachyptera risi* (Morton), 3. *Amphinemura sulcicollis* (Stephens), 4. *Siphonoperla burmeisteri* (Pictet), 5. *Leuctra hippopus* (Kempny), 6. *Capnopsis schilleri* (Rostock), 7. *Diura nanseni* (Kempny), 8. *Taeniopteryx nebulosa* (L.), 9. *Nemoura cinerea* (Retzius), 10. *Isoperla obscura* (Zetterstedt), 11. *N. avicularis* Morton, 12. *L. nigra* (Olivier), 13. *I. grammatica* (Poda), 14. *A borealis* (Morton), 15. *L. fusca* (L.)/*Leuctra* sp. 16. *L. digitata* Kempny, 17. *A. standfussi* Ris, 18. *Capniidae* 19. *Isoperla* sp.

The parameters also showed differences between seasons. Ephemeroptera had low diversity both in spring (H' = 0.59) and autumn (H' = 0.87), nd highest diversity in summer (H' = 1.54). Evenness indexes varied from 0.30 to 0.64 and followed the values of diversity. In spring *Baetis rhodani* (1) dominated the ephemeropteran fauna and the number of species was low. This led to a low species diversity as well as a low evenness index. Relatively high diversity of Ephemeroptera in summer was due to high numbers of several summer species such as *Baetis scambus* Eaton (10) and *Heptagenia joernensis* (Bengtsson) (9) and to less dominance of *Baetis rhodani*.

Plecoptera showed a relatively high species diversity both in winter (H' = 1.93), spring (H' = 1.87) and especially autumn (H' = 2.12). The corresponding evenness indices were 0.75, 0.73 and 0.83. While Ephemeroptera had the highest diversity in the summer, the Plecoptera showed the lowest index at that time (H' = 0.91). This was due primarily to the high numbers of *Leuctra fusca* (15) which totally dominated the plecopteran fauna at this time of the year (Fig. 2).

The variability between H' values on different occasions in the same season was also high, standard deviation varying from 0.29 to 0.61 in Ephemeroptera and from 0.15 to 0.48 in Plecoptera. As an example of this variation, the diversity of Ephemeroptera changed from 1.18 on September 13th to 0.31 on October 9th. This was due to the emergence of *Baetis scambus* and *Heptagenia joernensis* in between these two sampling occasions, and also to the species number falling from 12 in September to 6 in October.

As already mentioned the effect of species number (ln S) and evenness (J') on H' may vary depending on the species' abundance. The relative importance of these two components is examined in Table 4.

Table 4. Correlation coefficients between: 1) H' and ln S. 2) H' and J' for Ephemeroptera and Plecoptera.

Season	n	Ephemeroptera (1)	Ephemeroptera (2)	Plecoptera (1)	Plecoptera (2)
Winter (Dec.-March)	6	0.92	0.95	0.08	0.99
Spring (April-May)	6	0.53	0.98	0.39	0.76
Summer (June-Aug.)	6	0.29	0.98	0.51	0.97
Autumn (Sept.-Nov.)	5	0.84	0.97	0.31	0.95

Table 5. Correlation coefficients between Ephemeroptera H' values and Plecoptera H' values at different seasons. n.s. = not significant (at 95% level).

	n	k	p
Winter	5	0.30	n.s.
Spring	7	0.25	n.s.
Summer	6	−0.19	n.s.
Autumn	5	0.74	$p < 0.05$
Whole year	23	−0.13	n.s.

The diversity of both Ephemeroptera and Plecoptera showed a close correlation with the relative species' abundance (the evenness component) at all seasons. The correlation between the species richness component and diversity showed greater variability and was generally low. This component affected the diversity of the Ephemeroptera community in winter, and that of the Plecoptera community in summer. Evidently the diversity index both for the Ephemeroptera and the Plecoptera communities was primarily determined by the relative species abundance.

Correlation between diversity values of the two communities is examined in Table 5. The correlation between H' values of Ephemeroptera and Plecoptera was only significant during the autumn and negative during summer. For the whole year the diversities of Ephemeroptera and Plecoptera were negatively correlated. Thus the diversity of ephemeropteran and plecopteran communities shows little or no covariation.

DISCUSSION

As expected, Ephemeroptera and Plecoptera showed variation both in species richness, Shannon-Weaver index and evenness throughout the year. Ulfstrand (1975) found that similar diversity index values could result from rather divergent communities and argued for an evaluation of the role of the components of species richness and evenness when discussing diversity.

The present data showed that changes in relative abundances of species could change the diversity within short time intervals as well as between seasons. A high or low diversity or evenness index on one occasion has little predictive power on a later date r season at the same locality. Changes in relative abundance of species among Ephemeroptera and Plecoptera may to a great extent be due to the life cycle of the species considered (Brittain 1978, Lillehammer 1978). Species with a short growing period may during this period strongly influence diversity (cfr. *Baetis scambus, Heptagenia joernensis* and *Leuctra fusca* in the stream Sagelva). This is illustrated by the considerable changes in diversity and evenness during emergence and after egg hatching. Thus, a locality with a diverse community in one season may be comparitively poor at another. Diversity values based on one or a few sampling periods will therefore provide false information concerning the overall diversity. A corresponding inconsistency was found by Ulfstrand (1975) for Ephemeroptera and Plecoptera communities in streams in Swedish Lapland. These results illustrate that comparative analyses of diversity within or between localities should be based on samples from all seasons.

Seasonal changes in a species' bundance in one locality may also be due to several other factors than life cycles. Friberg et al. (1977) examined influence of ten environmental variables on the diversity of benthic communities. They found a low number of significant correlations between environmental and community parameters, and pointed out the possible significance of biotic factors.

The present results indicated clear differences between the ephemeropteran and plecopteran communities. Dominance of one or a few species was more common among the Ephemeroptera than in the Plecoptera. This led to lower diversity and evenness indices for the ephemeropteran community. The two groups also tended to have their highest species richness and diversity values at different seasons. While Ephemeroptera peaked in both species richness, diversity and evenness in summer, the Plecoptera showed their lowest values in this season.

The two groups seem to react differently to constellations of physical and biotic environmental or intrinsic factors, illustrated by the fact that diversity values of the groups were poorly or negatively correlated at different seasons and for the whole year.

The Ephemeroptera and Plecoptera were obtained in the same samples and thus inhabited closely similar environments. Environmental factors such as substratum, depth and water velocity (Ulfstrand 1967, Lillehammer 1974, Rabeni and Minshall 1977) may therefore be discounted when discussing differences between the ephemeropteran and plecopteran communities. The intrinsic characteristics of the populations seem to be the reason for the diversity differences.

I have argued that life cycles exert considerable influence on species abundance which is the most important component of the diversity both for Ephemeroptera and Plecoptera. However, population parameters such as biotic potential, mortality, interspecific and intraspecific competition may also influence the abundance of species and structure of the community.

Food habits and competition may be different in Ephemeroptera and Plecoptera species. Baekken (1981) found that relatively small changes in food composition may involve considerable shifts of micorhabitats. Large size variations of *B. rhodani* nymphs and their different spacing reduced the interaction both within *B. rhodani* and between the two detrivorous species *B. rhodani* and *Capnia pygmaea* Zetterstedt (Baekken 1981). In Sagelva *B. rhodani, B. scambus* and *Heptagenia dalecarlica* Bengtsson showed considerable variation in body size at any point in time (Arnekleiv 1981). In addition these species are partly separated in time. This may reduce potential interspecific competition.

The Plecoptera appear on the other hand, to show narrower feeding specializations (Ulfstrand 1975) and less variation in body size, leading to stronger interspecific interactions and competition. This may cause greater spacing in the microdistribution in the Plecoptera than among the Ephemeroptera. Ephemeroptera generally occupy a lower trophic level than many Plecoptera and produce large numbers of progeny (Brittain 1973, Cummins 1974, Ulfstrand 1975). In Sagelva large cohorts of nymphs of the most abundant Ephemeroptera species *(B. rhodani)* lowered the diversity index in autumn. Greater numerical fluctuations in the Ephemeroptera than the Plecoptera may be due to large cohorts of progeny among the Ephemeroptera and this may explain some of the differences found between the ephemeropteran and plecopteran community. There seems to be need for more experimental studies and biotic factors need to be placed more in the foreground to evaluate the significance of diversity and other community parameters.

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Ecological segregation of sympatric heteropterans on apple trees

NINA JONSSON

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This paper investigates the microhabitat and life history of sympatric heteropterans on apple trees in a Norwegian apple orchard. The herbivorous *Atractotomus mali* (Meyer-Dür), *Campylomma verbasci* (Meyer-Dür), *Orthotylus marginalis* Reuter, and *Psallus ambiguus* (Fallén) emerged successively in the spring. The nymphs occurred in higher numbers in clusters with flowers and leaves, than in clusters with leaves only. First to third instar nymphs lived under bud scales and among leaf and flower stalks. Older nymphs and adults lived exposed on leaves, fruit, and branches. Corresponding nymphal stages of the herbivorous species developed synchronously, the developmental stages were short. The predaceous *Anthocoris nemorum* (L.), *Blepharidopterus angulatus* (Fallén), and *Phytocoris tilia* (Fabricius) emerged in succession and later in the spring than did the herbivorous species. The developmental stages were significantly longer and less synchronous than those of the herbivorous species. First instar nymphs lived under bud scales and among leaf and flower stalks in the blossom clusters. Older nymphs and adults lived exposed on leaves, fruits, and branches. The relationship of life history patterns to prey defense and predator success is discussed.

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INTRODUCTION

A number of Heteroptera species live sympatrically on apple. Species like *Anthocoris nemorum* (L.), *Blepharidopterus angulatus* (Fallén), and *Phytocoris tilia* (Fabricius) are mainly predaceous, feeding on mites, psyllids, aphids, and mirids (Collyer 1952, 1967, Collyer & Massee 1958, Dixon & Russel 1972, Glen 1973, Hill 1957, Lord 1971). Species like *Atractotomus mali* (Meyer-Dür), *Campylomma verbasci* (Meyer-Dür), *Psallus ambiguus* (Fallén) are mainly herbivorous, and especially the nymphs suck plant juice from the leaves, and leaf and flower stalks. But, occasionally they prey on mites, aphids, and psyllids (McMullen & Jong 1970, MacPhee 1976, Morris 1965, Niemczyk 1978, Lord 1971, Sandford 1964). The mentioned heteropterans are numerically dominant in many Norwegian orchards (Austreng & Sømme 1980, Jonsson 1983a, Skånland 1981), and their life cycle might therefore be co-adapted. The life cycle of each of the species is well known (Austreng & Sømme 1980, Morris 1965, Niemczyk 1978, Skånland 1981). The nymphs hatch in spring, and in most species the adults die during autumn. However, less is known about the relative emergence patterns and microhabitat of coexisting herbivorous and predaceous heteropterans. Information about these relationships are important for better understanding of interspecific relations in heteropteran communities on apple trees.

Thus, I investigated the microhabitat and life cycle of coexisting herbivorous and predaceous heteropterans in an Norwegian apple orchard during two consecutive years, and discuss difference in life history strategies of the herbivorous and predaceous species.

STUDY AREA

The study was carried out in an apple orchard at Gaustad, Oslo, South-Eastern Norway. The apple orchard, which was approximately 2500 m^2, consisted of 39 apple trees, alined in three rows. The dominating varieties were Cox's Pomona, Åkerø, and Signe Tillisch. The trees were all well-kept and approximately 60 years old. No pesticides had been applied to the orchard during a period of three years prior to this study.

SAMPLING

To investigate the emergence of nymphs in spring and to study their habitat in detail, I picked all nymphs living in 50—100 clusters with flowers and leaves, and leaves only every 2—3 days during the periods 30 April—13 June 1980 and 2 May—10 June 1981. On each sampling day, clusters were picked from all the apple trees in the orchard. An equal numbers of clusters were sampled from the sunny and shady sides of the trees.

To investigate the life cycle of the heteropterans present, samples from 26 branches on the sunny and 26 branches on the shady side were collected using Steiner's beating method (Steiner 1962). The samples were taken every 4—8 days during 6 May—7 November 1980 and 13 May—4 November 1981.

The sampled material was examined and counted under a stereoscopic microscope (10X).

RESULTS

A total of 4166 specimens of 33 species was sampled during 1980 and 2055 specimens of 21 species during 1981. In 1980 the species *A. nemorum, A. mali, B. angulatus, C. verbasci*, and *P. ambiguus* were dominant (sensu Geiler 1960), each species comprising more than 5% of the total sample size, and the species *O. marginalis* and *P. tilia* were subdominant as they made up between 2—5% of the total sample size. In 1981 the species *A. mali, B. angulatus, C. verbasci, O. marginalis*, and *P. ambiguus* were dominant, and *A. nemorum* and *P. tilia* were subdominant.

The nymphs were significantly more abundant in clusters with flowers and leaves than in those with leaves only ($P < 0.05$, Mann-Whitney U-test) (Table 1). The nymphs of *A. mali, C. verbasci, O. marginalis*, and *P. ambiguus* made up approximately 95% of the total sample in both flower and leaf clusters, whereas nymphs of *A. nemorum, B. angulatus*, and *P. tilia* made up the remaining 5%.

The emergence patterns of the numphs and adults of the dominating species in relation to the development of the apple blossoms were similar in both years (Fig. 1), and the eggs of the various species hatched in the same succession in both years. The nymphs of *O. marginalis* and *P. ambiguus* emerged first, a few days earlier than *A. mali* and *C. verbasci*. The first and second instar stages of these species lived mainly within the blossom clusters, under bud scales, within curled leaves and flowers, and at the base of leaf and flower stalks. The third instar nymphs were more mobile and more exposed, living at the base of the leaf and flower stalks, and on the leaves. Nymphs in fourth and fifth instar stages were even more mobile, living on leaves, leaf stalks, and on the fruit.

The first instar nymphs of *A. nemorum, B. angulatus*, and *P. tilia* were also resident under bud scales, and at the base of the leaf and flower stalks in the blossom clusters. The second instar stages, however, were more mobile, and *A. nemorum* and *P. tilia* were mainly observed on the leaves, leaf and flower stalks, and branches, whereas *B. angulatus* lived mainly on leaves and flower stalks. The third to fifth instar stages of all species were very mobile and lived exposed on leaves, leaf stalks, fruit, and branches.

The nymphal and adult stages of *A. mali, C. verbasci, O. marginalis*, and *P. ambiguus* were significantly shorter than those of *A. nemorum, B. angulatus*, and *P. tilia* (Fig. 1, $P < 0.05$, Mann-Whitney U-test). The adult stage of *C. verbasci* seemed to last 10 weeks longer in 1980 than in 1981. *A. nemorum* hibernated in the adult stage; only adult females were sampled early in spring 1980, and both adult females and males were sampled in spring 1981. In 1980, *A. nemorum* might have two generations as a few first and fifth instar nymphs were sampled late in autumn. The other dominant species hibernated in the egg stage and had one generation per year.

Table 1. Number of nymphs in leaf clusters and blossom clusters in different developmental stages, sampled on apple trees in 1981.

Date	Blossom	No. of blossom clusters	No. of nymphs	No. of leaf clusters	No. of nymphs
19 May	Ballon	35	25	20	0
24 May	Flowering	55	27	49	4
27 May	Flowering	37	41	60	5
30 May	Flowering	65	68	33	8
2 June	80% faded flower	40	69	10	2
Total		232	230	172	19

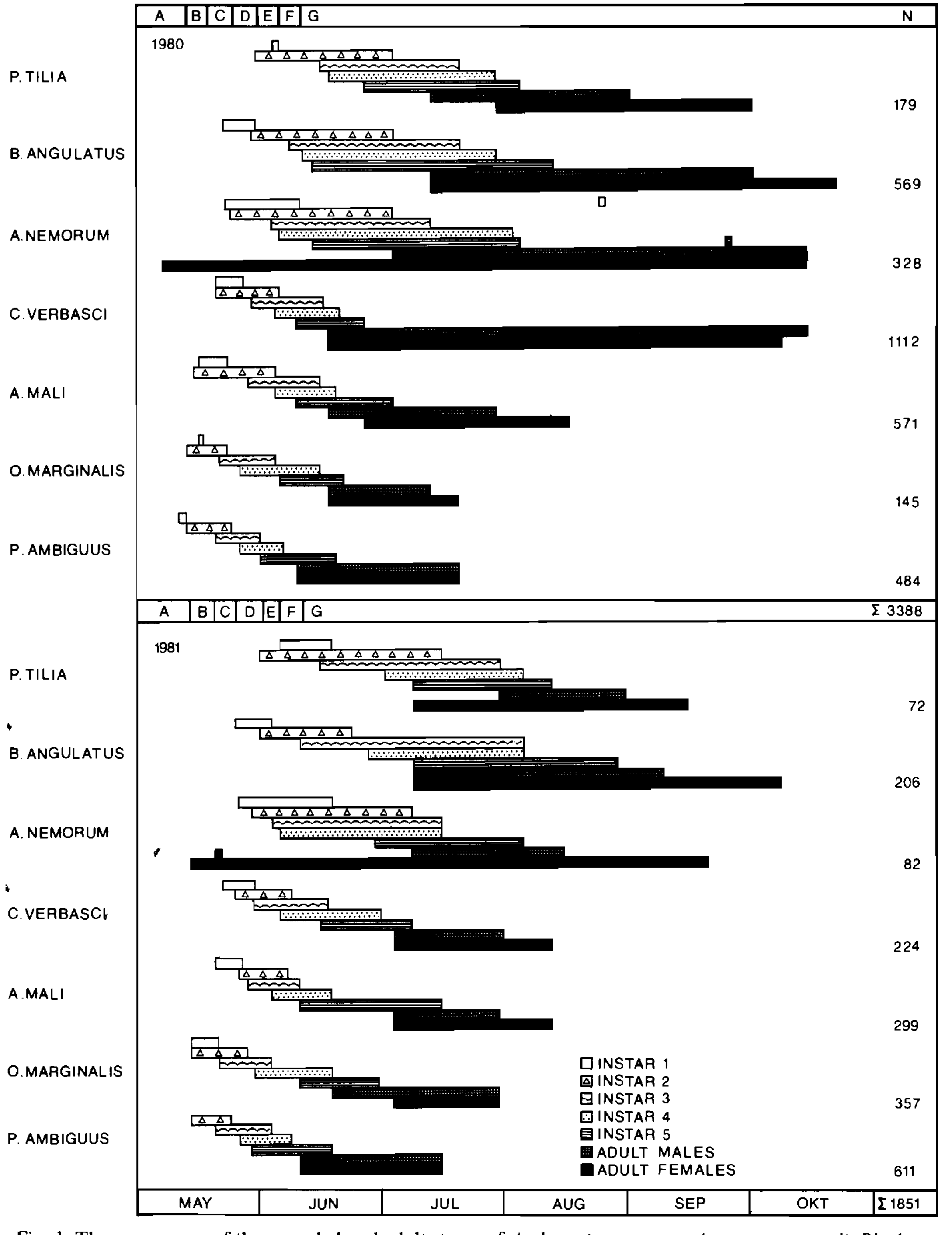

Fig. 1. The occurrence of the nymphal and adult stages of *Anthocoris nemorum, Atractotomus mali, Blepharidopterus angulatus, Campylomma verbasci, Orthotylus marginalis, Phytocoris tilia,* and *Psallus ambiguus* in relation to the development of the apple blossoms at Gaustad, Oslo in 1980 and 1981. The developmental stages of the apple blossoms are indicated as A: leaf emergence, B: green clusters, C: ballon, D: flowering, E: 80 % faded flower, F: faded flower, G: fruit.

DISCUSSION

The herbivorous nymphs emerged early in spring concurrently with the blossom clusters of the apple trees. The young nymphs are small and almost immobile, and are thus vulnerable to both predation and hostile weather. But the nymphs live sheltered within the newly emerged blossom clusters of the apple trees. Newly formed blossoms have thin cuticle (Miller 1973), which is easily penetrated by the proboscis of the young nymphs. If needed, animal protein can be obtained by sucking nymphs of *Psylla mali,* which also live in the apple blossoms (Jonsson 1983b). The highly synchronized development of the herbivorous nymphs may indicate lax competition for food and space (Pianka 1974). Furthermore, the rapid nymphal development probably counteracts predation, since large individuals are more difficult to catch than smaller ones. The life history characterized by an early hatching of the eggs in the spring, synchronous nymphal development, and a short life span, suggests a prey strategy which minimize the effects of predation.

The predaceous nymphs emerged later in the spring, when their prey species were abundant. Their nymphal development was less synchronous and several instars occurred simultaneously, compared with the herbivorous species. Different instar nymphs used different habitats. The heterogeneous development counteracts intraspecific competition, this indicate that food is limited for these species (Hairston 1964). The life history of the predaceous bugs characterized by hatching of the eggs in late spring, concurrent occurrence of several instar stages, and a long life span, suggests a predator strategy, which maximizes utilization of the food supply.

The successive occurrence of various species, and the earlier emergence of the prey than the predator species may be developed through natural selection. It is a general phenomenon that predators and parasites emerge after prey or host. As the various nymphal stages occupy different microhabitats, the successive emergence decreases interspecific competition and allows each species to increase their population density. Parallel to this, Grant & MacKay (1969) and MacKay (1972, 1979), have documented how related Trichoptera species avoid interspecific conflicts by differing in emergence time. Although there is much overlap in the life cycle of the heteropterans studied, successive occurrence of heteropterans may be another example on how an insect community is shaped through natural selection.

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Carabidae and Staphylinidae (Col.) in swede and carrot fields in northern and south-western Norway

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Andersen, A. 1985. Carabidae and Staphylinidae (Col.) in swede and carrot fields in northern and south-western Norway. *Fauna norv. Ser. B, 32,* 12—27.

During May—Oct. 1978—82 about 2200 carabids and 6600 staphylinids were caught in pitfall traps in ten swede and carrot fields in Tromsø and at Jæren. The activity density for each species caught in each field is given, as well as the time for its maximum activity. For the most numerous species the seasonal changes are also given in histograms, with comments on their reproduction cycles.

Among the carabid species caught at Jæren 60%, in Tromsø only 6.7%, were autumn breeders. The staphylinids were more dominant relative to the carabids in Tromsø than at Jæren. Higher carabid activity density occurred in swede than in carrot fields at Jæren, while the staphylinid activity density was approximately the same in the two types of crop. The Sørensen index of similarity for Tromsø—Jæren was 26.

The dominant species in Tromsø were the carabids *Bembidion bruxellense* Wesmaël, *B. bipunctatum* (L.) and *Loricera pilicornis* (Fabricius), and the staphylinids *Aloconota gregaria* (Erichson), *Oxypoda umbrata* (Gyllenhal) and *Atheta fungi* (Gravenhorst). The five most numerous carabid species made up 90% of the material, compared to the staphylinids' 80%. At Jæren the dominant species were the carabids *Bembidion lampros* (Herbst), *Calathus melanocephalus* (L.) and *Clivina fossor* (L.), and the staphylinids *A. gregaria, Oxypoda exoleta* Erichson and *A. fungi*. The ten most numerous carabid and the nine most numerous staphylinid species made up 88% and 86% of the material, respectively.

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INTRODUCTION

Carabids and staphylinids are important predators of several pest species in agricultural fields (Thiele 1977, Andersen et al. 1983). In a recent publication Andersen (1982b) discussed the carabid and staphylinid fauna of cruciferous fields in south-eastern Norway. The purpose of the present investigation was to get information on the composition of the fauna of carabids and staphylinids in agricultural fields also in other parts of Norway. It is part of a project evaluating the importance of natural enemies of the dipterous pests the turnip root fly, *Delia floralis* Fallén, and the cabbage root fly, *D. radicum* (L.), in cruciferous crops, and the carrot fly, *Psila rosae* (Fabricius), in carrots.

LOCALITIES

In northern Norway the experimental fields were situated at The Agricultural Research Station Holt in the district of Tromsø (EIS : 162). Two swede fields (later treated together) of the variety 'Stenhaug' were investigated in 1978 and one field in each of the years 1979 and 1980. The fields were located less than 250 m apart and 2—300 m away from the sea. The soil in Tromsø consisted mainly of sand and gravel, in 1980 the content of peat was high. Each field was 400 m^2, surrounded by fields of cabbage, carrots, swedes and grass. No insecticides were used in the investigated swede fields, but some of the surrounding fields were treated. The swedes were irrigated only occasionally during drought in June. The previous crop was grass, except for swedes prior to one of the fields in 1978.

In south-western Norway one swede and one carrot field were investigated each year in 1979—1981. In addition one swede field was investigated in 1982.

The swede fields, of the variety 'Bangholm Ruta', were situated at The Agricultural Research Station Særheim in the district of Klepp at Jæren (EIS : 7), less than 500 m apart and about 6 km in from the sea. The soil consisted of moraine with a low content of organic matter and clay. Each field was about 1500 m^2 (in 1982 only 340 m^2) of a swede field of 1600—3500 m^2. The fields were surrounded by barley, grass and vegetables. Several kinds of insecticides were used in the swede field each year, mainly granules of chlorfenvinphos and isofenphos. Irrigation was used only in a small part of the field in 1980. The previous crop was always grass.

The carrot fields, of the variety 'Nantes Duke', were each year a 3500 m^2 part of a commercial carrot field of 1.0—1.6 ha at Jæren. The fields were situated less than 4 km apart, about 6 km from the swede fields and less than 1 km from the sea. The soil consisted of light sand, in 1979 with some organic matter. In 1979 fenthion was sprayed twice in July, otherwise no insecticides were used. No irregation occurred. The fields were surrounded by barley, gravel roads, pine forest and sand dunes. The previous crop was always grass.

The yearly mean temperature in Tromsø was 2.9°C, at Jæren 7.4°C. At Jæren, the swedes and carrots were sown in April or May, in Tromsø the swedes were sown in a greenhouse and planted out 5—15 June.

MATERIAL AND METHODS

Pitfall traps containing 4% formalin and with an upper diameter of 66 mm were used. Normally nine traps were put up in (three) straight lines in each field. The distance between traps was 5 m in Tromsø and 10—16 m at Jæren (except in 1982: 2.5—5.5 m). The trapping period in each field is shown in Fig. 1. Because trapping in the swede field at Jæren in 1982 did not start until the end of July, results from this year were excluded when calculations and comparisons were made. In the present publication mean number of specimens per 100 trap days during the trapping period is used to measure the activity density. For a closer description and discussion of the method used see Andersen (1982b).

The material consists of 544 carabids of at least 15 species and 2618 staphylinids of at least 54 species from Tromsø, and 1645 carabids of at least 30 species and 4037 staphylinids of at least 55 species from Jæren. The nomenclature follows Silfverberg (1979), with names used in Lindroth (1960) with later corrections by Strand (1970, 1977) in brackets. Because parts of the *Aleocharinae*-material were not classified to species, diversity indices were not calculated for staphylinids.

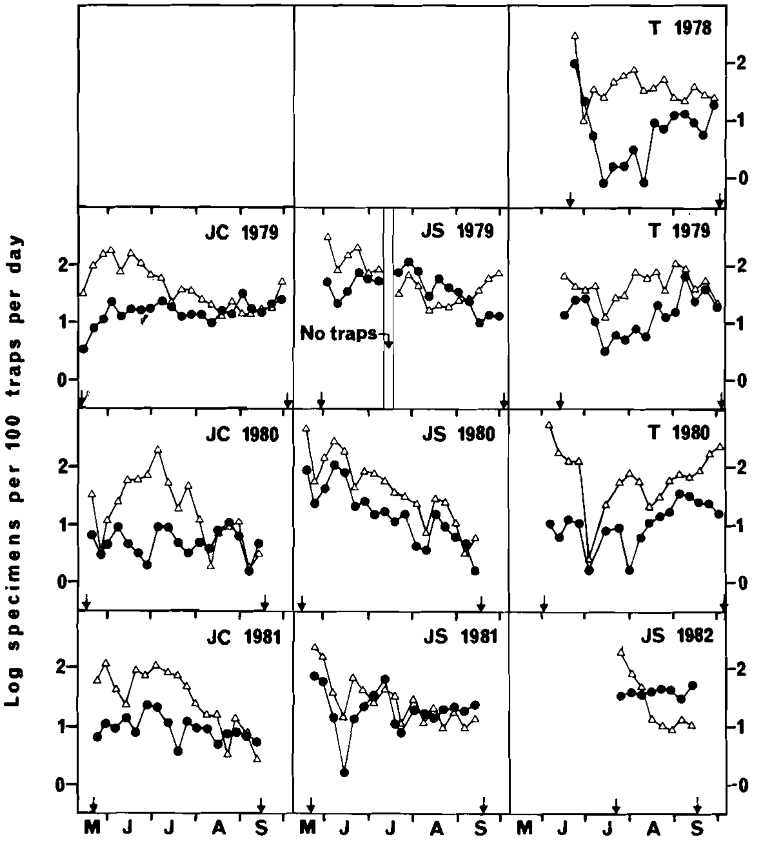


Fig. 1. Total activity density for carabids (●) and staphylinids (△) in each of the ten fields. Arrows indicate beginning and end of the trapping periods. T = Tromsø, swedes. JC = Jæren, carrots. JS = Jæren, swedes.

RESULTS AND DISCUSSION

When referring to the fauna of carabids and staphylinids in south-eastern Norway in the present discussion, the source is Andersen (1982b). Fig. 1 shows the total activity density of carabids and staphylinids in the ten fields. In Tromsø almost all the carabids caught were spring breeders, making up 93.9% of the material. The four species *Amara quenseli* (Shönherr), *A. torrida* (Panzer), *Calathus melanocephalus* (L.) and *Patrobus assimilis* Chaudoir, probably having a two-year developmental cycle so far to the north (Lindroth 1945, van Dijk 1972), made up 6.1% of the material. The only autumn breeder was one specimen of *Amara apricaria* (Paykull) caught in 1978, giving a ratio of individuals of autumn to spring breeders of only 0.002. This strongly confirms that autumn breeding carabids are less common in colder climates (Thiele 1977). Part of this tendency may, however, be explained by the soil, as spring breeders are known to prefer sand (Thiele 1977). In accordance with the high catch of spring breeders, the curves in Fig. 1 show a peak in June during reproduction, a lower catch in July, and again a peak in Aug.—Sept., when the next generation emerges. Because trapping was not started until June, part of the probable reproductive activity in May—June was not recorded. High catches in June, a drop in the beginning of July and a rise again in (July—)Aug. are seen also with the staphylinids (Fig. 1).

At Jæren the percentage of autumn breeding carabid species was 64 in carrots and 58 in swedes. These are high percentages compared with those found in cruciferous fields in south-eastern Norway (39—44) (Andersen 1982b), and fit in well with the fact that autumn breeders are more common in areas with Atlantic climate (Thiele 1977). The maximum activity density of staphylinids at Jæren occurred in June—July, corresponding well with the finds in south-eastern Norway.

Tables 1—4 show the total catch of the different species for each field. At the bottom of the tables also the number of specimens and the minimum number of species found per field are given, as well as the number of trap days and the diversity index (for carabids only).

The Sørensen index of similarity between Tromsø and Jæren was 26, between carrot and swede fields at Jæren 73, and between fields in the same locality it varied between 52—59 in Tromsø, 54—67 in carrot and 70—73 in swede fields at Jæren. This clearly shows an expected difference between the faunas in Tromsø and at Jæren, while faunas in carrot and swede fields at Jæren were quite similar.

To evaluate the similarity between agricultural fields in south-western and south-eastern

Table 1. Mean activity density, given in specimens per 100 trap days for carabids caught in Tromsø 1978—1980, together with their main activity months. r ≤ 0.1 per 100 trap days.

Species	1978	1979	1980	Main activity months
Amara apricaria (Paykull)	r			6—7
A. interstitialis Dejean	0.8	1.5	0.4	6,9
A. quenseli (Schönherr)		0.5		8—9
A. torrida (Panzer)	0.3		0.4	6,8
Bembidion bipunctatum (L.)	1.2	2.9	1.7	6,8—9
B. bruxellense Wesmaël	8.1	8.3	6.8	6,9
B. sp.	r			9
Calathus melanocephalus (L.)	0.3		1.2	6
Elaphrus riparius (L.)	0.7	1.0	r	6—7
Loricera pilicornis (Fabricius)	0.5	3.2	1.0	6,9
Notiophilus biguttatus (Fabricius)	r		1.0	9
Patrobus assimilis Chaudoir			r	7
Pelophila borealis (Paykull)	r		r	6,9
Pterostichus adstrictus Eschscholtz	0.1			6,8
P. oblongopunctatus (Fabricius)	r	r	r	9
Number of specimens	228	178	138	
Number of species	13	7	11	
Number of trap days	1872	1017	1071	
Shannon-index	1.31	1.47	1.25	

Table 2. Mean activity density, given in specimens per 100 trap days for staphylinids caught in Tromsø 1978—1980, together with their main activity months. r ≤ 0.1 specimens per 100 trap days.

Species	1978	1979	1980	Main activity months
Acrotona (Atheta) aterrima (Gravenhorst)			r	6
Aleochara bilineata Gyllenhal	1.2	2.0	0.7	7—8
A. brundini Bernhauer	2.7	2.8	1.5	7—8
A. sparsa Heer			r	10
Aleocharinae spp.	1.4	r	0.3	—
Aloconota (Atheta) gregaria (Erichson)	28.2	24.8	49.6	6,8—9
Amischa analis (Gravenhorst)	0.2	r	r	7,9
Anotylus (Oxytelus) nitidulus (Gravenhorst)		r		6
A. (O.) rugosus (Fabricius)	r		6.1	6,9
A. (O.) sp.	0.2			6
Anthophagus omalinus Zetterstedt	0.3			8
Aploderus caelatus (Gravenhorst)	r	r		8—9
Arpedium quadrun (Gravenhorst)			r	9
Atheta atramentaria (Gyllenhal)		r		6
A. debilis (Erichson) ♂	r			6
A. fungi (Gravenhorst)	2.2	6.4	4.0	6—9
A. graminicola (Gravenhorst)	2.0	0.5	2.3	6,8—9
A. malleus Joy *(hygrobia* Thomson) ♂	0.5	1.5	0.9	6,8—9
A. melanocera (Thomson) ♂	0.4	0.3	r	6,8
A. (Philhygra) spp. ♀	0.9	2.0	2.0	—
A. islandica (Kraatz)/eremita (Rye) ♀			r	6
Autalia puncticollis Sharp	0.3			8—9
Bryoporus cernuus (Gravenhorst)	0.4			7,9
Carpelimus (Trogophloeus) sp.		r		6
Deliphrum tectum (Paykull)		r		9
Eucnecosum (Arpedium) brachypterum (Gravenhorst)	r			7
Gabrius sp. ♀	r			9
Megarthrus depressus (Paykull)	r			6
Mycetoporus sp.		r		6
Olophrum assimile (Paykull)	1.2		10.5	9—10
Omalium caesum Gravenhorst	r			9
O. excavatum Stephens	0.4			6,8
O. rivulare (Paykull)	0.8			7
O. septentrionis Thomson	r	r	0.5	6—10
Othius angustus Stephens *(melanocephalus* Gravenhorst)	0.3	0.2		7—8
O. lapidicola Kiesenwetter			r	6
O. myrmecophilus Kiesenwetter	r			7
Oxypoda nigricornis Motschulsky		0.4		8
O. spectabilis Märkel			r	10
O. umbrata (Gyllenhal)	2.3	5.1	29.4	6
Parocyusa (Chilopora) ribicunda (Erichson)	0.1		r	7—8
Philonthus carbonarius (Gravenhorst) *(varius* Gyllenhal)		0.2		7—8
P. nigriventris Thomson	r			9
P. ochropus (Gravenhorst) *(concinnus* Gravenhorst)		1.5	0.4	7
P. pachycephalus Nordmann *(sordidus* Gravenhorst)		0.2		9—10
P. sp.	r			8
Platystethus nodifrons Mannerheim		0.2		7,9
Quedius molochinus (Gravenhorst) *picipennis* Paykull)	r	r		7
P. nitipennis (Stephens)	0.5	r	1.1	6—10
Stenus sp.	0.2			6,9
Tachinus corticinus Gravenhorst	1.4	0.2	1.5	9
T. lignorum (L.)			r	10
T. pallipes Gravenhorst			0.2	9—10
T. signatus (Gravenhorst) *rufipes* Degeer)	r			9
Tachyporus pusillus Gravenhorst			0.9	9—10
Number of specimens	914	497	1207	
Number of species	35	26	26	
Number of trap days	1842	1017	1071	

Table 3. Mean activity density, given in specimens per 100 trap days for carabids caught at Jæren 1979—1982, together with their main activity months. r ≤ 0.1 specimens per 100 trap days.

	Carrots			Swedes				Main activity
Species	1979	1980	1981	1979	1980	1981	1982	months
Agonum muelleri (Herbst)				r	0.4	0.9		6—7
A. sexpunctatum (L.)					r			9
Amara apricaria (Paykull)	r	0.2	r		r		1.0	7—8
A. bifrons (Gyllenhal)			0.9	r	0.3	0.2	1.5	6—8
A. fulva (Degeer)	0.2	0.5	0.8		r	r		7—8
A. plebeja (Gyllenhal)	0.2		r	0.3				6
Bembidion lampros (Herbst)	2.0	0.2		11.2	12.9	5.3		6
B. bruxellense Wesmaël				0.2	0.4			6
B. sp.		r						7
Calathus erratus (Sahlberg)	0.2	1.2	0.8					8
C. fuscipes (Goeze)	0.3	0.2	r	7.7		0.5	0.6	7—8
C. melanocephalus (L.)	0.4	0.3	2.8	6.7	0.8	2.8	3.0	7—8
C. micropterus (Duftschmid)		0.4	r					6
Carabus nemoralis Müller	r	r	r	0.2	0.2			6
Clivina fossor (L.)	3.3		r	1.0	5.2	1.3	2.4	5—8
Cychrus caraboides (L.)			r					7
Harpalus affinis (Schrank)		0.2		r	0.2			6—7
H. latus (L.)				r				6
Harpalus quadripunctatus Dejean							0.1	8
H. rufipes (Degeer)	r	r	0.3	0.3	r		0.1	7
Loricera pilicornis (Fabricius)	0.9	0.8	2.0	3.8	0.8	0.5		6—7
Nebria brevicollis (Fabricius)	2.3		r	2.1	0.3	1.7	10.6	8—9
Notiophilus biguttatus (Fabricius)	0.2		r	0.2		r		8—9
N. germinyi Fauvel				0.2				7
Patrobus atrorufus (Strøm)	1.5		0.2	1.3	0.2	7.9	19.3	7—9
Pterostichus melanarius (Illiger)	2.4			6.3		0.7	1.0	7—8
P. niger (Schaller)				r				8
Synuchus vivalis (Illiger)	0.2			0.4	0.3		0.6	7—8
Trechus quadristriatus (Schrank)	0.7			2.3	2.2	2.3	3.0	8
Trechus secalis (Paykull)			0.3	0.3	1.1	r		6—8
Number of specimens	197	46	92	481	283	255	291	
Number of species	17	12	17	22	18	14	12	
Number of trap days	1323	1116	1053	1071	1116	1053	672	
Shannon-index	2.26	2.15	2.03	2.20	1.75	2.00	1.67	

Table 4. Mean activity density, given in specimens per 100 trap days for staphylinids caught at Jæren 1979—1982, together with their main activity months. r ≤ 0.1 specimens per 100 trap days.

	Carrots			Swedes				Main activity
Species	1979	1980	1981	1979	1980	1981	1982	months
Acidota crenata (Fabricius)	r	r						5,8
Acrotona (Atheta) aterrima (Gravenhorst)	0.3	r	0.5		r	0.2		5—6
Aleochara bipustulata (L.)	0.5		0.6	0.3				5—7
A. sp.	0.2							5—6
Aleocharinae spp.	0.2	r		0.3				—
Aloconota (Atheta) gregaria (Erichson)	23.4	5.2	12.1	30.3	32.9	11.1	28.2	5—8
Amischa analis (Gravenhorst)	5.7	0.4	1.9	9.1	8.7	4.7	1.5	6

Anotylus (Oxytelus) rugosus (Fabricius)	5.6	0.2	0.8	4.4	3.1	2.3	0.1	5–7
A. (O.). tetracarinatus (Block)	r							5
Atheta atramentaria (Gyllenhal)	0.5	0.4	r	r		r		6–8
A. celata (Erichson)		r						8
A. elongatula (Gravenhorst)	2.4	0.3		0.2	2.2	0.4	0.3	5–6,8
A. fungi (Gravenhorst)	7.3	3.6	10.0	5.7	3.2	5.4	10.4	6–7
A. graminicola (Gravenhorst)					r			8
A. macrocera (Thomson)						r		7
A. palustris (Kiesenwetter)	r							5
A. (Philhygra) sp. ♀						0.1		7–8
Bledius sp.		r						5
Dinaraea (Atheta) angustula (Gyllenhal)	r							6
Geostiba (Sipalia) circellaris (Gravenhorst)	r	0.7	0.4	0.2		r	0.1	6
Gyrohypnus angustatus Stephens	0.5	0.2	1.0	1.9	1.1	r		6
Lathrobium fulvipenne Gravenhorst	0.3					r		6–7
L. geminum Kraatz	0.2							6–7
Mycetoporus splendidus (Gravenhorst)		0.2	r					5–6
M. sp.	0.7			4.1	2.8	0.2		—
Oligota sp.			r					6
Othius angustus Stephens *(melanocephalus* Gravenhorst)	r		1.0	r	r		0.1	7
O. myrmecophilus Kiesenwetter		0.4	0.3		r	r	0.1	8
Oxypoda brachyptera (Stephens)	0.7	0.4	0.3	0.3	0.2	1.3		6
O. exoleta Erichson	0.3	r	0.5	14.3	21.4	11.0	3.6	5–6
O. umbrata (Gyllenhal)	0.2				0.4			5–7
O. spp.		1.7	6.6					—
Philonthus carbonarius (Gravenhorst) *(varius* Gyllenhal)	1.8		0.6	0.7	0.2	0.4	0.4	5–7,9
P. cognatus Stephens *(fuscipennis* Mannerheim)	r		r					6,9
P. decorus (Gravenhorst)				r				9–10
P. marginatus (Strøm)		r			r			6
P. pachycephalus Nordmann *(sordidus* Gravenhorst)	r		0.6		r			6
P. splendens (Fabricius)			r			0.3	0.1	5–8
P. varians (Paykull)	r							8
Platystethus arenarius (Fourcroy)			r					6
Quedius molochinus (Gravenhorst) *picipennis* Paykull)		0.3		r				6
Q. sp.		r						7
Stenus clavicornis (Scopoli)		r						5–6
S. sp.		r						7
Tachinus corticinus Gravenhorst	0.5	17.4	3.6	0.2	0.5			6–7
T. laticollis Gravenhorst	r							9
T. signatus (Gravenhorst) *rufipes* Degeer)	1.6		0.2	1.2	1.0	2.0	0.1	5–6
Tachyporus chrysomelinus (L.)	0.5	0.9	0.9	0.4	0.4	r		6–7
T. hypnorum (Fabricius)	0.2			r	r	r		7
T. obtusus (L.)	0.4	0.9	0.8	r	0.2			6–7
T. pulchellus Mannerheim	r			r				7
T. pusillus Gravenhorst	2.3	0.2	2.5	0.4	0.4	0.9		5–6
T. solutus Erichson	0.2							6
T. sp.			0.2					—
Tinotus morion (Gravenhorst)			r					5
Xantholinus linearis (Olivier)		r	0.2					5–7
X. tricolor (Fabricius)					r			6
Number of specimens	753	382	485	797	884	431	305	
Number of species	36	28	31	24	24	21	13	
Number of trap days	1323	1116	1053	1071	1116	1053	672	

Norway the Sørensen index of similarity was calculated between the fields at Jæren and the fields at Jeløy, Ås and Ski published by Andersen (1982b). The values were 48 for Jæren—Jeløy, 51 for Jæren—Ås and 56 for Jæren—Ski, clearly indicating similarities between the faunas of the two geographical areas. In all calculations of the Sørensen index of similarity, individuals not classified to species in two locations were treated as different species.

Tables 5 and 6 show the five most numerous species in each locality. The following species were among the ten most numerous carabids in both carrot and swede fields at Jæren: *Calathus melanocephalus*, *Bembidion lampros* (Herbst), *Clivina fossor* (L.), *Loricera pilicornis* (Fabricius), *Nebria brevicollis* (Fabricius) and *Calathus fuscipes* (Goeze). The same holds for the staphylinid species *Aloconota gregaria* (Erichson), *Atheta fungi* (Gravenhorst), *Amischa analis* (Gravenhorst), *Anotylus rugosus* (Fabricius), *Atheta elongatula* (Gravenhorst) and *Tachyporus pusillus* (Gravenhorst).

The carabids *C. melanocephalus*, *B. lampros* and *C. fossor* were also among the ten most numerous species in the three localities in south-eastern Norway, the same holds for the staphylinids *A. gregaria*, *A. fungi*, *A. analis* and *A. rugosus*. Tromsø had few dominating species in common with Jæren or south-eastern Norway. The carabid *C. melanocephalus* was among the ten most numerous species in all three areas, the same holds for the staphylinids *A. gregaria*, *A. fungi* and *A. rugosus*.

Table 5. The most numerous species in Tromsø.

Abundance no.	Carabids	Staphylinids
1	*Bembidion bruxellense*	*Aloconota gregaria*
2	*B. bipunctatum*	*Oxypoda umbrata*
3	*Loricera policornis*	*Atheta fungi*
4	*Amara interstitialis*	*Olophrum assimile*
5	*Elaphrus riparius*	*Aleochara brundini*

Table 6. The most numerous species at Jæren.

Abundance no.	Carrots	Swedes
	CARABIDS	
1	*Loricera pilicornis*	*Bembidion lampros*
2	*Calathus melanocephalus*	*Calathus melanocephalus*
3	*Clivina fossor*	*Patrobus atrorufus*
4	*Nebria brevicollis*	*Calathus fuscipes*
5	*Calathus erratus*	*Clivina fossor*
	STAPHYLINIDS	
1	*Aloconota gregaria*	*Aloconota gregaria*
2	*Tachinus corticinus*	*Oxypoda exoleta*
3	*Atheta fungi*	*Amischa analis*
4	*Amischa analis*	*Atheta fungi*
5	*Anotylus rugosus*	*Anotylus rugosus*

The diversity index for carabids is shown at the bottom of Table 1 and 3. The mean index at Jæren (2.07) was close to that for cruciferous fields in south-eastern Norway (1.95). The mean index in Tromsø was 1.34.

In Tromsø the mean yearly activity density for carabids varied between 12—18 specimens per 100 trap days each year, for staphylinids between 49—113. The values for carabids correspond with the lower ones in south-eastern Norway, but those for staphylinids are quite high compared to south-eastern Norway. The conclusion is that the staphylinids dominated more relative to the carabids in Tromsø than in south-eastern Norway.

At Jæren, the activity density for carabids in the carrot fields was low, varying between 4—15 each year. In the swede fields, the activity density varied between 24—45, values comparable to those in cruciferous fields in south-eastern Norway. In the fields at Jæren the activity density of the staphylinids varied between 34—79, with no marked differences in numbers between carrot and swede fields. These values also correspond well with those in south-eastern Norway.

In Tromsø, mostly the same carabid and staphylinid genera dominated as in south-eastern Norway, although with different species. Carabids of the genus *Harpalus* were, however, not caught in Tromsø, and the staphylinid genus *Tachyporus* appeared with only one species, making up only 0.4 % of the staphylinid material as compared to six species and 3.9 % at Jæren and seven species and 6.7 % in south-eastern Norway. The reverse is the case for the staphylinid subfamily Omaliinae. In Tromsø, nine species of this subfamily were caught, making up 6.6 % of the staphylinid material, as compared to only one species and 0.1 % at Jæren and eight species and 1.2 % in south-eastern Norway. The differences can be explained by the colder climate in Tromsø, eliminating the southern species, but giving good conditions for the northern ones.

Also between Jæren and south-eastern Norway typical differences exist. Among the carabids only four species of the genus *Harpalus* were caught at Jæren, making up 1.1% of the material, as compared to seven species and 6.1% in south-eastern Norway. *Bembidion quadrimaculatum* (L.), dominating in the fields in south-eastern Norway, was absent at Jæren. It does not belong to the fauna of western Norway (Lindroth 1960). Among the staphylinids only two species belonging to the genus *Aleochara* were caught at Jæren, making up 0.4% of the material, as compared to seven species and 7.9% in south-eastern Norway. No *Gabrius*-species were caught at Jæren, as compared to four in south-eastern Norway.

The staphylinid species *Atheta graminicola* (Gravenhorst), *Dinaraea angustula* (Gyllenhal) and *Oxypoda exoleta* Erichson are new to Rogaland, coastal part (RY), and *Atheta debilis* (Erichson), *A. malleus* Joy and *Philonthus ochropus* (Gravenhorst) are new to Troms, coastal part (TRY).

Different kinds of insecticides were used at Jæren in the carrot field in 1979 and in the three swede fields. As insecticides kill carabids and staphylinids along with the pests (Thiele 1977, Andersen 1982a), the applications have had some effect on the trapping data in these fields. However, as the experiments were not designed to evaluate the effects of the insecticides, this will not be discussed further.

The total number of carabid species caught in Tromsø and the carrot and swede fields at Jæren were 15, 23 and 26 respectively, the same for staphylinids being at least 54, 53 and 35. The five most numerous carabid and five staphylinid species from each of the localities (for carabids in Tromsø only three species) are treated separately in the following. Numbers given in brackets are mean number of specimens per 100 trap days per year, calculated from numbers in Tables 1—4. Breeding periods and habitat preferences for carabids not specifically mentioned are taken from Lindroth (1945).

Carabids

Bembidion bipunctatum (L.) was the second most numerous carabid species in Tromsø, making up 12.9% of the material. The mean activity density per year was 1.9. Andersen (1980) also found the species in Tromsø and numerous other parts of northern Norway. It probably reproduces in May—June, mainly before the trapping started. The maximum activity density was found in Aug.—Sept. (Fig. 2), this is probably the next generation that emerges. One callow specimen caught 1 Sept. 1980 also indicates this. It has not previously been found as a dominating species in agricultural fields. Further investigations are needed to establish whether it is a common field species in northern Norway.

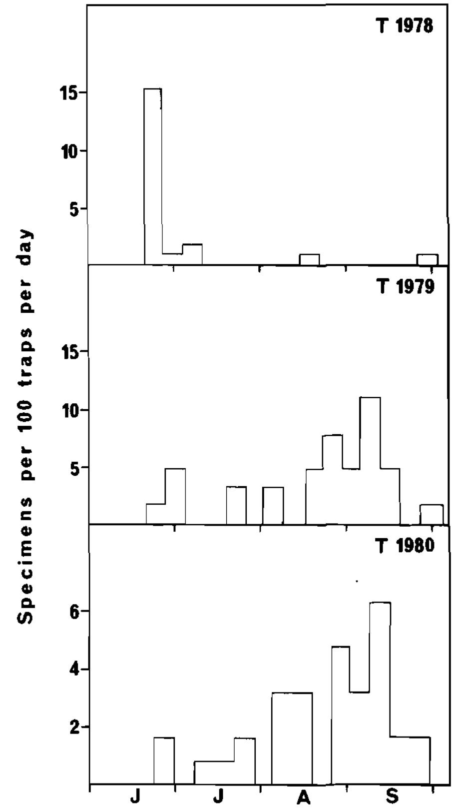


Fig. 2. Activity density for *Bembidion bipunctatum* in Tromsø.

The most numerous carabid in Tromsø was *Bembidion bruxellense* Wesmäel, making up 56.6% (!) of the material. The mean activity density (7.7) corresponds well with those for dominating *Bembidion*-species in southern Norway. Andersen (1980) also found the species in Tromsø and in numerous other parts of the provinces of Troms and Nordland. Maximum activity density occurred in June and Sept. (Fig. 3). It reproduces in May—June, and more than 30 callow specimens caught in Aug.—Oct. belong to the next generation emerging in the autumn. The species was caught in small numbers in the swede fields at Jæren (Table 3), and it was rare in cruciferous fields in south-eastern Norway. It is rarely a dominating species in European fields (Thiele 1977), but Holopainen (1983) found it to be dominating in cruciferous fields in central Finland.

Bembidion lampros (Herbst), the most numerous carabid caught at Jæren, made up 25.7% of the material. It was ranked as no. 6 in carrots (0.7) and no. 1 in swedes (9.8). The maximum activity density was

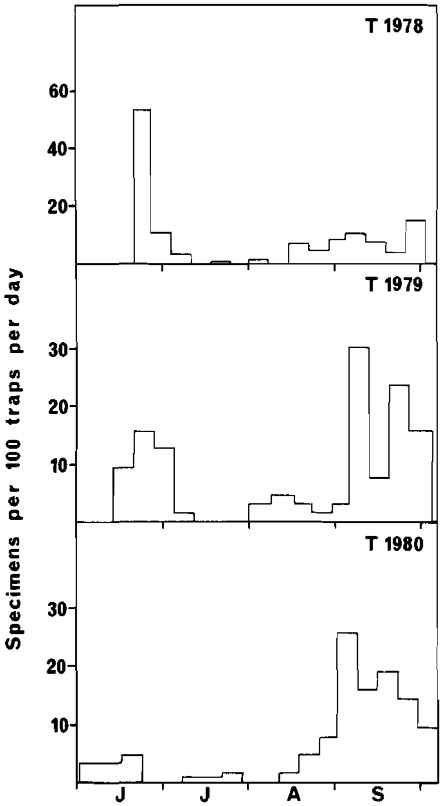


Fig. 3. Activity density for *Bembidion bruxellense* in Tromsø.

found during reproduction in (May—)June (Fig. 4), while few specimens were caught in the autumn. The activity density corresponds well with that found in cruciferous crops in south-eastern Norway.

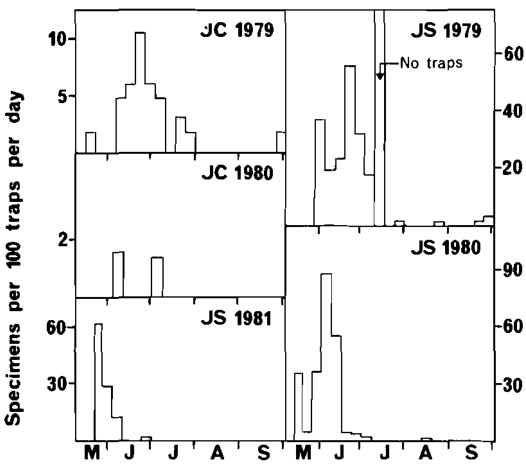
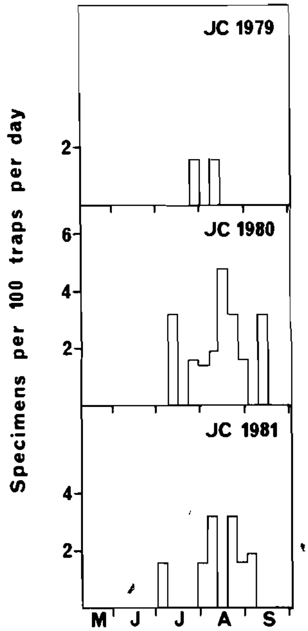


Fig. 4. Activity density for *Bembidion lampros* at Jæren.

Fig. 5. Activity density for *Calathus erratus* in carrot fields at Jæren.



Calathus erratus (Sahlberg) made up 1.7% of the material at Jæren. It was ranked as no. 5 in carrots (0.7), but was not caught at all in the swede fields. Maximum activity density was found during reproduction in Aug. (Fig. 5), higher than that found in cruciferous fields in south-eastern Norway. This typical heath species has sometimes been caught in European fields, although rarely dominating (Trittelvitz and Topp 1980, Holopainen 1983).

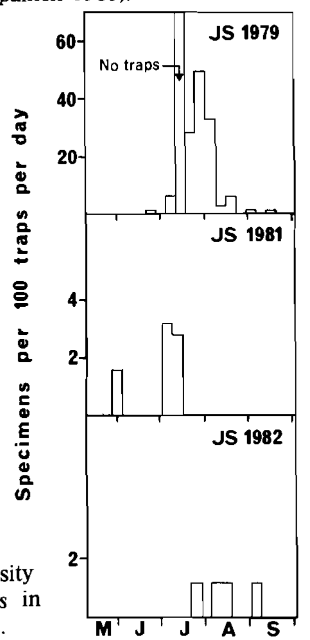


Fig. 6. Activity density for *Calathus fuscipes* in swede fields at Jæren.

Calathus fuscipes (Goeze) made up 7.0% of the material at Jæren, and was ranked as no. 9 in carrots (0.2) and no. 4 in swedes (2.7). The species, although eurotypic, abandons pure sand, which could explain the low catch in the carrot fields. The maximum activity density appeared in July—Aug. (Fig. 6), when it reproduces. It was trapped more frequently at Jæren than in the cruciferous fields in south-eastern Norway. The species is common in European fields (Thiele 1977).

Calathus melanocephalus (L.) was the second most numerous carabid caught at Jæren, making up 10.9% of the material. It was ranked as no. 2 in both carrot (1.2) and swede fields (3.4). In Tromsø it was ranked as no. 6 (0.5). Maximum activity density at Jæren was found in July (Fig. 7), when it reproduces, and two callow specimens were caught in June. The species, also trapped numerously in cruciferous fields in south-eastern Norway, must be one of the typical dominating field carabids in most parts of Norway. It is a common field species also in European fields (Thiele 1977).

Clivina fossor (L.), the third most numerous carabid caught at Jæren, made up 9.4% of the material and was ranked as no. 3 in carrots (1.1) and no. 5 in swede fields (2.5). The maximum activity density occurred during reproduction in June (Fig. 8). Four callow specimens caught 28 July—11 Aug. indicate the next generation emerging, although trapped in numbers only in 1982. It avoids pure sand, and accordingly was trapped least frequently in the carrot fields in 1980 and 1981 (Table 3). The activity density was comparable with that in cruciferous fields in

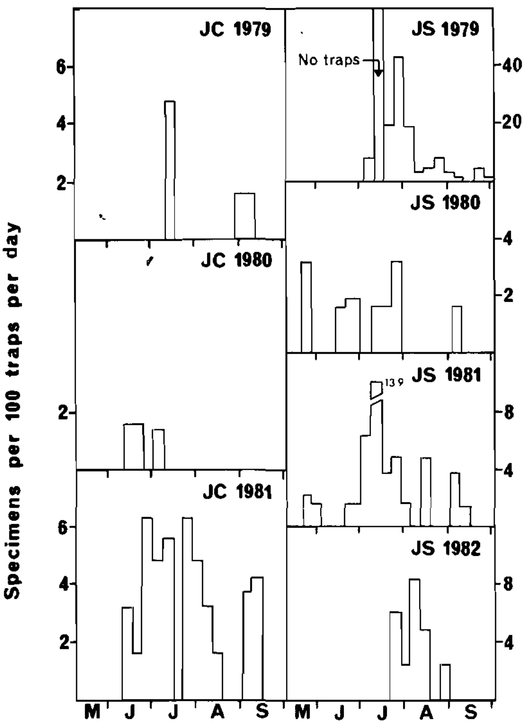


Fig. 7. Activity density for *Calathus melanocephalus* at Jæren.

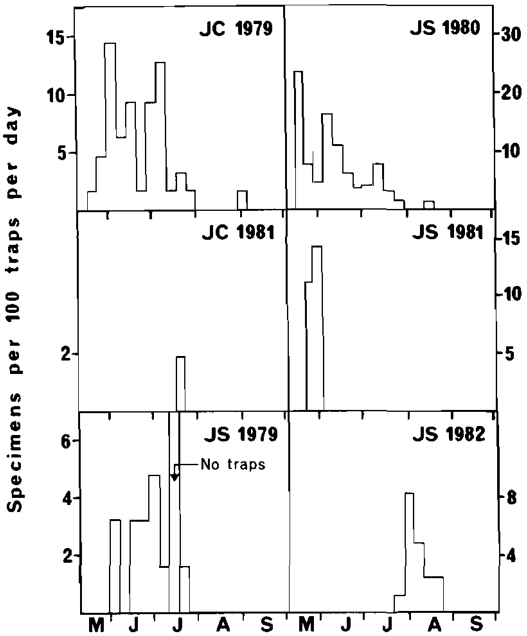


Fig. 8. Activity density for *Clivina fossor* at Jæren.

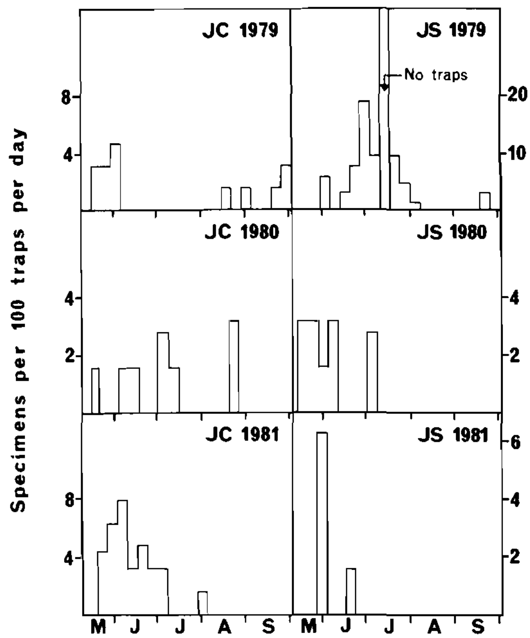


Fig. 9. Activity density for *Loricera pilicornis* at Jæren.

south-eastern Norway. It is a common species also in European fields (Thiele 1977).

Loricera pilicornis (Fabricius) made up 7.2% of the material at Jæren, and was ranked as no. 1 in carrots (1.2) and no. 8 in swedes (1.7). The maximum activity density occurred in May—June (Fig. 9), when it reproduces. In Tromsø it made up 9.7% of the material, was ranked as no. 3 (1.6), and the activity density was high in June and again in Aug.—Sept. (Fig. 10). Also in northern Norway it probably reproduces in May—June, but whether a part of the population reproduces in Aug.—Sept., as supposed for several carabid species in northern Scandinavia (Lindroth 1945), needs more detailed research. A suggested avoidance of pure sand was not confirmed, as it was trapped numerously in the carrot fields at Jæren. The activity density was high compared to that in south-eastern Norway. It is a common species in European agricultural fields (Thiele 1977).

Nebria brevicollis (Fabricius), making up 6.4% of the material at Jæren, was ranked as no. 4 in carrots (0.8) and no. 9 in swedes (1.4). It was caught mainly in Aug.—Sept. (Fig. 11), when it reproduces. Two callow specimens were caught in June. The species

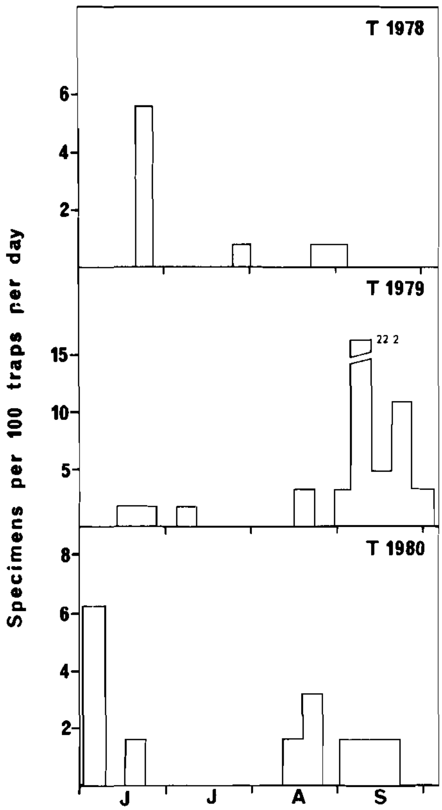


Fig. 10. Activity density for *Loricera pilicornis* in Tromsø.

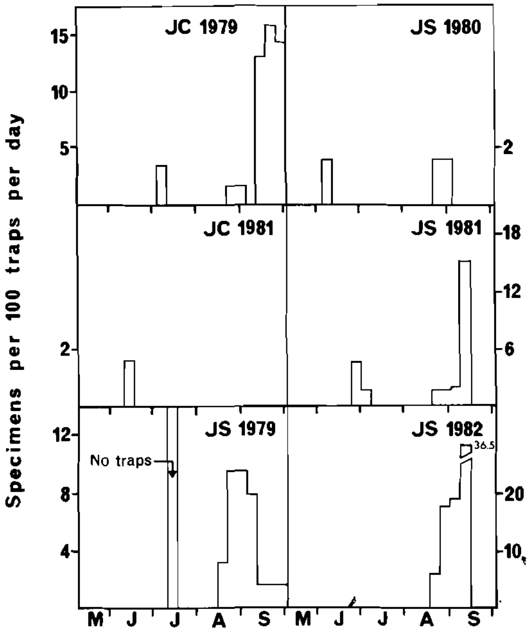


Fig. 11. Activity density for *Nebria brevicollis* at Jæren.

was rare in south-eastern Norway, but common in European fields (Thiele 1977).

Patrobus atrorufus (Strøm) made up 8.9% of the material at Jæren. It was ranked as no. 7 (0.6) in car-

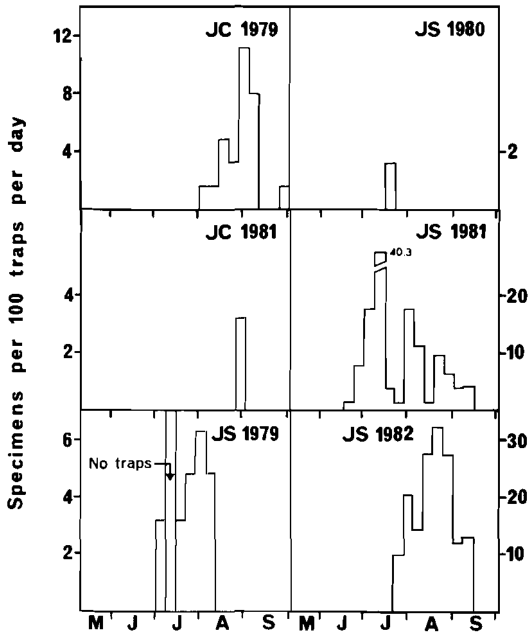


Fig. 12. Activity density for *Patrobus atrorufus* at Jæren.

rots and no. 3 in swedes (3.1). Maximum activity density occurred during reproduction in July—Sept. (Fig. 12). The species was rarely caught in cruciferous fields in south-eastern Norway. It is usually a rare species in European fields (Thiele 1977), but Holopainen (1983) found it dominant in cruciferous fields in central Finland.

Staphylinids

Aleochara brundini Bernhauer made up 3.6 % of the staphylinid material in Tromsø, and was ranked as no. 5 (2.3). Maximum activity density occurred in July—Aug. (Fig. 13). It parasitizes dipterous species (Palm 1972), among them probably the turnip root fly, *Delia floralis*, common in cruciferous crops in Norway. In July—Aug. the species probably searched for pupae of the turnip root fly to parasitize. It is a northern species, and was not found in southern Norway.

Aloconota gregaria (Erichson) was the most numerous species in all fields (!), making up 50.1 % of the material in Tromsø and 35.0 % at Jæren. The mean activity density per year was somewhat higher in Tromsø (34.2) than in the carrot (13.6) and swede fields (24.8) at Jæren. Maximum activity density at Jæren usually occurred in June (Fig. 14), when it reproduces. Callow specimens were caught mainly in July—Aug., indicating the next generation emerging. In Tromsø the main activity periods were in June and Aug.—Sept. (Fig. 15). Fifteen callow specimens caught in Aug.—Sept. indicate that the species also in northern Norway reproduces in the spring with the next generation emerging in the autumn. The activity density corresponds well with that found in cruciferous fields in south-eastern Norway. *A. gregaria* must be a dominating staphylinid in agricultural fields in most parts of Norway. It is common also in European fields (Geiler 1959/60).

Amischa analis (Gravenhorst) made up 9.2% of the material at Jæren and was ranked as no. 4 in carrots (2.7) and no. 3 in swedes (7.5). It was trapped in small numbers in Tromsø (Table 4). Maximum activity density occurred in May—June (Fig. 16), when it probably reproduces. High activity density in Aug.—Sept. some years may be the next generation emerging. The activity density is somewhat lower than that found in cruciferous fields in south-eastern Norway. Previously Geiler (1959/60) and Topp and Trittelvitz (1980) have caught it in various fields.

Anotylus rugosus (Fabricius) made up 5.1 % of the material at Jæren, and was ranked as no. 5 in both carrots (2.2) and swedes (3.3). Maximum activity density occurred during reproduction in June (Fig.

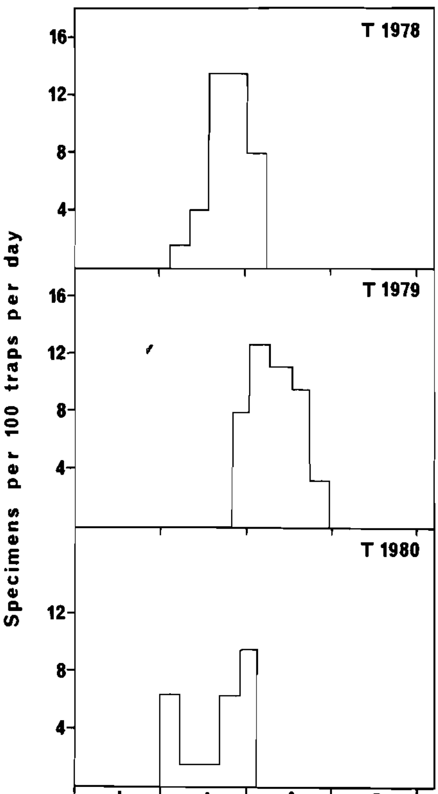


Fig. 13. Activity density for *Aleochara brundini* in Tromsø.

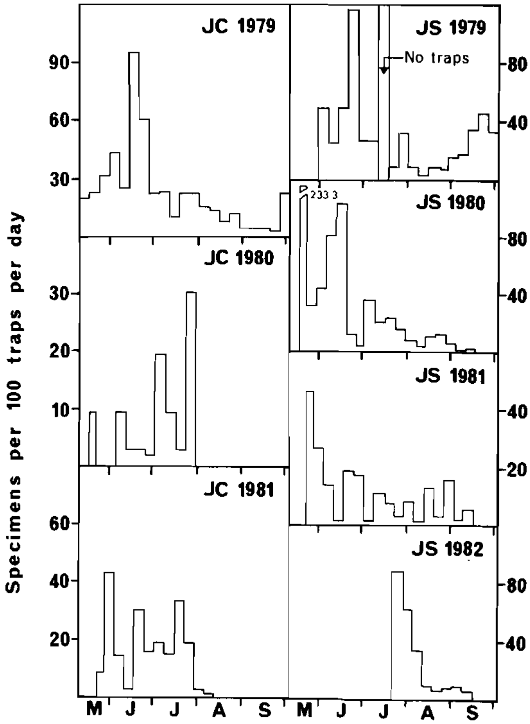


Fig. 14. Activity density for *Aloconota gregaria* at Jæren.

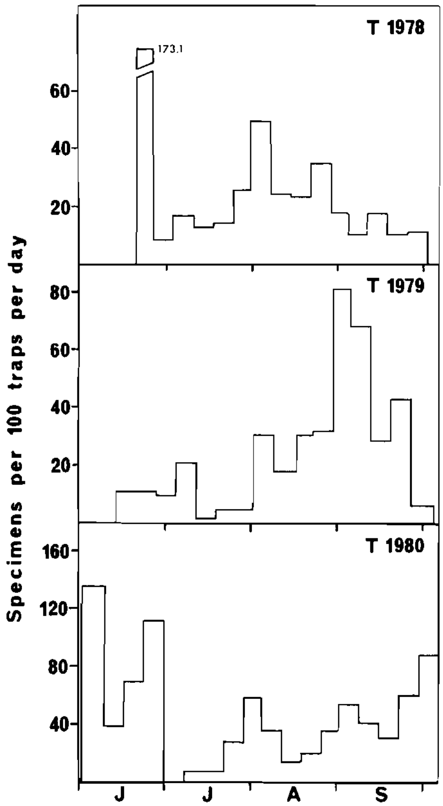


Fig. 15. Activity density for *Aloconota gregaria* in Tromsø.

17), and five callow specimens caught in July—Aug. belong to the next generation emerging. In Tromsø the species was trapped mainly in 1980 (Table 4), and made up 2.5% of the material. It was ranked as no. 7 (2.0). Three callow specimens were caught in Aug.—Sept. The activity densities fit in well with that in cruciferous fields in south-eastern Norway. It is also a common species in European agricultural fields (Tischler 1958, Geiler 1959/60).

Atheta fungi (Gravenhorst) made up 10.6% of the material at Jæren, and was ranked as no. 3 in carrots (7.0) and no. 4 in swedes (4.8). Maximum activity density occurred in June—July (Fig. 18), and two callow specimens belonging to the next generation caught in Aug.—Sept. indicate reproduction in June—July. The maximum activity density at Jæren appears earlier than in south-eastern Norway, and is probably due to the milder climate in south-western Norway, as Topp (1975) has shown that the pre-oviposition period of *A. fungi* is temperature dependent. In Tromsø it was the third most numerous species, making up 5.6% of the material. The activity density (4.2) was almost as high as at Jæren (Fig. 19). *A. fungi* was caught numerously also in cruciferous fields in south-eastern Norway, and must be one of the domi-

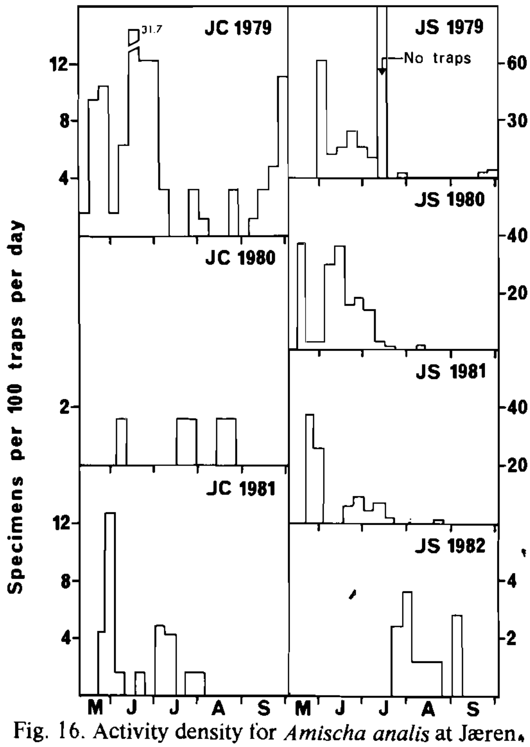


Fig. 16. Activity density for *Amischa analis* at Jæren.

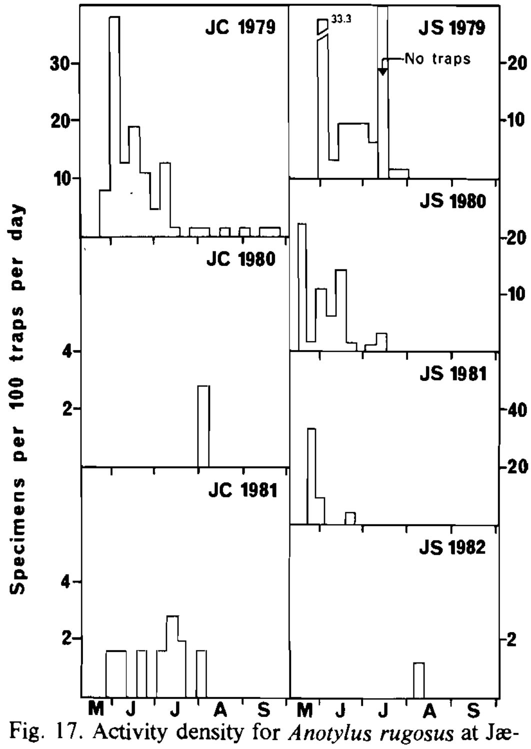


Fig. 17. Activity density for *Anotylus rugosus* at Jæren.

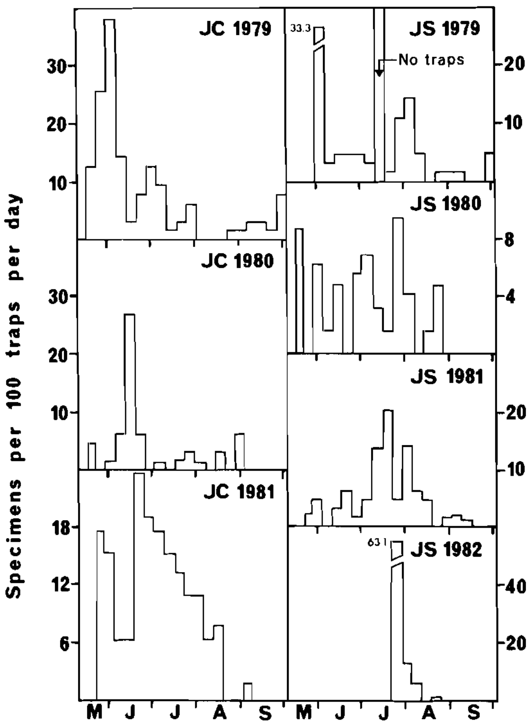


Fig. 18. Activity density for *Atheta fungi* at Jæren.

nating staphylinids in agricultural fields in most parts of Norway. It is common also in European fields (Geiler 1959/60, Topp and Trittelvitz 1980).

Olophrum assimile (Paykull) made up 5.2% of the material in Tromsø, and was ranked as no. 4 (3.9). Maximum activity density occurred in Sept.—Oct. (Fig. 20). The species has not previously been found dominating in agricultural fields, although caught in low numbers in cruciferous fields in south-eastern Norway.

Oxypoda exoleta Erichson was the second most numerous species at Jæren, making up 13.9% of the material. It was ranked as no. 2 in the swede fields (15.6), but was rare in the carrot fields (Table 2). Maximum activity density usually occurred in June (Fig. 21), when it probably reproduces. It was rarely caught in cruciferous fields in south-eastern Norway, but Pietraszko and Clercq (1978) found it numerously in wheat fields in Belgium.

Oxypoda umbrata (Gyllenhal) was the second most numerous species in Tromsø, making up 15.7% of the material. The yearly mean activity density was 12.3, and the maximum activity density occurring in June 1980 indicates reproduction (Fig. 22). The species was rarely caught at Jæren (Table 4). It was not caught in cruciferous fields in south-eastern Norway, but Geiler (1959/60) mentions it as common in agricultural fields.

Tachinus corticinus Gravenhorst made up 6.6% of the material at Jæren. It was ranked as no. 2 in the

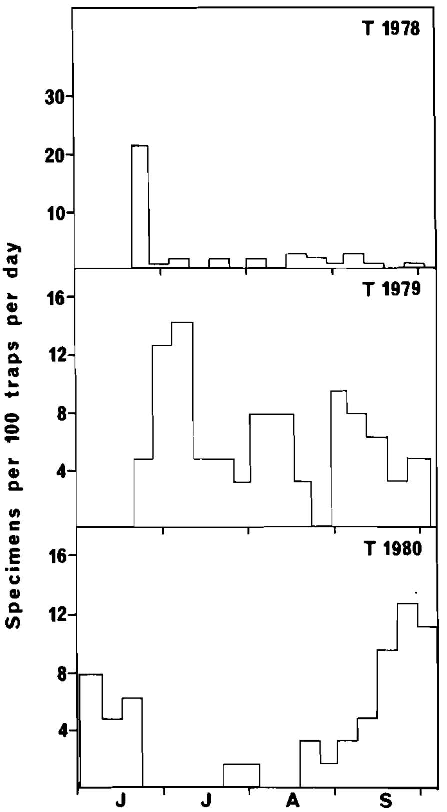


Fig. 19. Activity density for *Atheta fungi* in Tromsø.

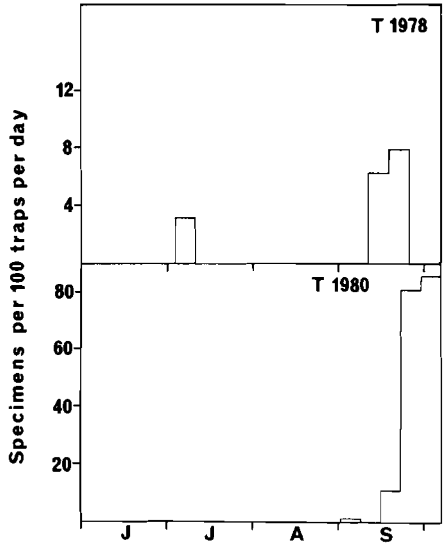


Fig. 20. Activity density for *Olophrum assimile* in Tromsø.

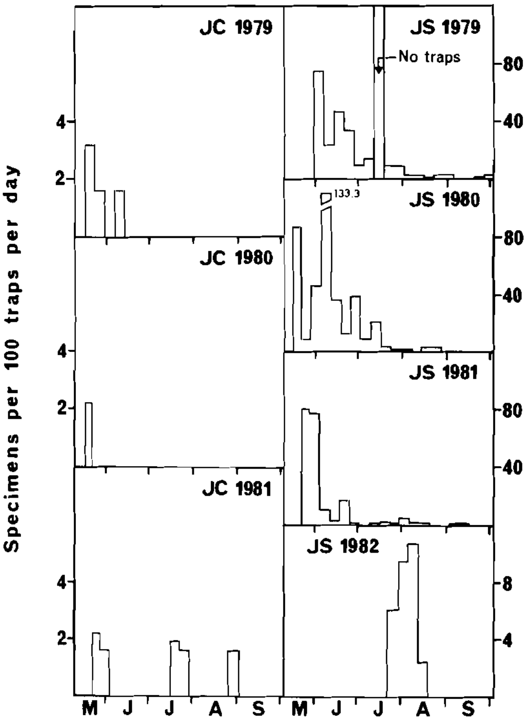


Fig. 21. Activity density for *Oxypoda exoleta* at Jæren.

carrot fields (7.2), but was rarely caught in the swede fields (Table 2). Maximum activity density occurred in June—July (Fig. 23), when also six callow specimens were caught. The specimens emerging in June—July probably reproduce the same summer, but whether the species is mono- or bivoltine is uncertain. The species was trapped regularily in Tromsø, and made up 1.7% of the material. It was ranked as no. 10 (1.0). According to Geiler (1959/60) it is common in agricultural fields, and Topp and Trittelvitz (1980) found it in maize and rye fields on sandy soil.

In Tromsø, three of the separately treated carabid species together with *Amara interstitialis* Dejean and *Elaphrus riparius* (L.) made up 90.1% of the material. Two of the separately treated staphylinids together with *Aleochara bilineata* Gyllenhal, *Atheta graminicola* and *A. malleus* made up 80.2% of the material. At Jæren eight of the treated carabid species together with *Pterostichus melanarius* (Illiger) and *Trechus quadristriatus* (Shrank) made up 88.1% of the material, and six of the treated staphylinids together with *Atheta elongatula*, *Tachinus signatus* (Gravenhorst) and *Tachyporus pusillus* made up 85.8% of the material.

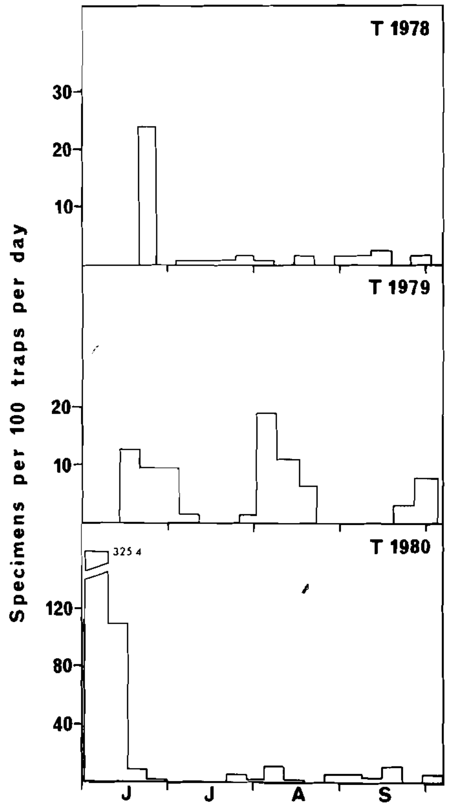


Fig. 22. Activity density for *Oxypoda umbrata* in Tromsø.

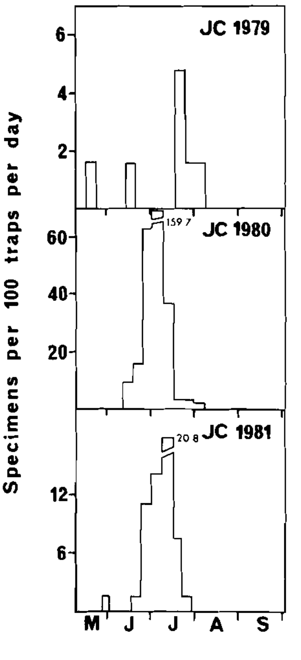


Fig. 23. Activity density for *Tachinus corticinus* in carrot fields at Jæren.

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Species composition and seasonal activity patterns of Carabidae (Col.) in a small deciduous forest in western Norway

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Kålås, J.A. 1985. Species composition and seasonal activity patterns of Carabidae (Col.) in a small deciduous forest in western Norway. — *Fauna norv. Ser. B, 32:* 28—32.

Species composition and seasonal activity patterns of Carabidae was studied by pitfall traps during a one year cycle in a small deciduous forest at Kålås, Western Norway. A total of 26 Carabidae species were caught, and the two most abundant species were *Pterostichus oblongopunctatus* (Fabricius) and *Nebria brevicollis* (Fabricius). Seasonal activity pattern is showed for twelve species. Of these, eight were found to be «autumn breeders», and four were «spring breeders». The activity patterns found correspond to a great extent to findings in Denmark and southern Sweden, but small differences were observed for some species. Totally the seasonal activity patterns in this study seems to be more similar to the findings in Denmark than in southern Sweden.

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INTRODUCTION

The carabids of deciduous forests have been investigated in some European countries (see Thiele 1977), but in Norway the knowledge on this subject is scanty.

Information on patterns in seasonal variation in activity of carabids are available for different species and from different areas (Larsson 1939, Lindroth 1945, Jörum 1965, Thiele 1977, Refseth 1980, Houston 1981, Andersen 1982), but no material has been published from western Norway.

The present paper deals with the composition of the carabid community in a small deciduous forest in western Norway, and the annual activity patterns is presented for 12 species.

STUDY AREA, MATERIAL AND METHODS

Carabid beetles were collected at Kålås, near Bergen, western Norway (60°33'N, 5°23'E). The study area was a small south-facing deciduous forest (150 x 50 meters) about 80 m.a.s.l.. The vegetation was dominated by hazel *Corylus avellana* with some aspens *Populus tremula* and ash trees *Fraxinus excésior*. The forest floor was mostly covered by dead leaves and the ground vegetation was poorly developed. The forest was surrounded by cultivated land.

The pitfall traps used were 100 mm deep glass cups with an upper diameter of 60 mm. The cups were dug flush with the soil and filled with 4% formalin. They were protected from rain and birds by a 10 x 10 cm aluminium plate about 5 cm above the ground. 15 traps were put out the 28 of March 1982 and collected the 27 of March 1983. The traps were arranged in a straight line about 5 meters apart and were emptied about once a month.

«Activity density» is the number of specimens per 100 trap days during the trapping period. The breeding season of the various species was defined from the variation in activity density (Larsson 1939, Thiele 1977, Refseth 1980).

The total material consisted of 1745 carabids of 26 species. The nomenclature follows Silfverberg (1979).

RESULTS AND DISCUSSION

The community

Tab. 1 shows the total numbers of different carabids caught in the pitfall traps. A total of 26 different species was caught. The most numerous genera were *Carabus* and *Pterostichus* with 4 and 6 species, respectively. All species caught were previously known from the region (Lindroth 1945). The carabid community is to a

Tab. 1. Numbers of different carabidae caught in 15 pitfall traps at Kålås during one year.

Pterostichus oblongopunctatus (Fabricius)	626
Nebria brevicollis (Fabricius)	227
Patrobus atrorufus (Strøm)	153
Calathus micropterus (Duftschmid)	126
Carabus nemoralis Müller	114
Pterostichus melanarius (Illiger)	96
Pterostichus versicolor (Sturm)	80
Carabus problematicus Herbst	73
Pterostichus niger (Schaller)	68
Notiophilus biguttatus (Fabricius)	53
Carabus coriaceus (L.)	48
Trechus secalis (Paykull)	19
Calathus fuscipes (Goeze)	16
Pterostichus nigrita (Paykull)	13
Harpalus quadripunctatus Dejean	7
Loricera pilicornis (Fabricius)	5
Synuchus vivalis (Illiger)	4
Carabus violaceus L.	3
Cychrus caraboides (L.)	3
Leistus rufescens (Fabricius)	2
Notiophilus germinyi Fanvel	2
Pterostichus vernalis (Panzer)	2
Trichocellus placidus (Gyllenhali)	2
Agonum mülleri (Herbst)	1
Clivina fossor (L.)	1
Harpalus latus (L.)	1
	1745

great extent determinated by vegetation, temperature and moisture (Löser 1972). The composition of carabids in the study area fits best to the carabid community found in the plant communities *Fagetalia Silvaticae* (Thiele 1977) which have neutral to slightly acid soil with equable and moist microclimate. *Nebria brevicollis* (Fabricius) is a typical species of these communities.

However, some of the species found are characteristic for the plant communities *Quercetalia Robori — Petraeae* with some more acid soil and drier and warmer microclimate (ex. *Calathus micropterus* (Duftschmid) (Thiele 1977).

Species with different demand to moisture are represented. *Pterostichus oblogopunctatus* (Fabricius) was the dominating species in the traps (36%). This eurytopic and eurythermic forest species is also the most abundant in central Europe, and it is a dry loving species (Thiele 1977). The relative abundant species *Nebria brevicollis* (13%) and *Patrobus atrorufus* (Strøm) (9%) are moisture loving species. As the forest was surrounded by cultivated land, typical agricultural species as *Loricera pilicornis* (Fabricius) and *Clivina fossor* (L.) were also caught. The forest seems to hold carabid species with different demand on vegetation, moisture and temperature, but the species which demand forest, neutral to slightly acid soil and moist microclimate are dominating.

Annual activity pattern

Different pattern are found in the seasonal activity of carabids. Lindroth (1945) suggested the use of the therms «adult hibernator» and «larval hibernator» to characterize different reproduction strategies. The designations «spring breeders» and «autumn breeders» are also used to distinguish between different types of reproduction in carabids (Larsson 1939). From the pitfall

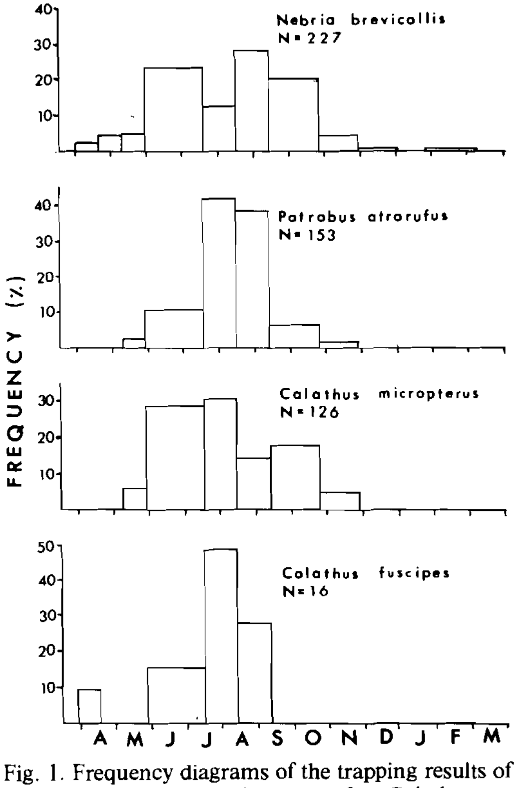

Fig. 1. Frequency diagrams of the trapping results of *Nebria brevicollis, Patrobus atrorufus, Calathus micropterus* and *C. fuscipes* at Kålås.

material it was possible to show the activity pattern of 12 species in the study area. 8 of these were «autumn breeders» and 4 were «spring breeders».

Nebria brevicollis. The characteristic diapause (Gilbert 1958) of this species in July/August was also found in this study (Fig. 1), and it corresponds to the findings in Denmark (Jörum 1976), Great Britain (Penney 1966, 1969) and Germany (Thiele 1969). The species had a long activity period from April until December, and one animal was even caught in February. The activity density indicate that the species also in my study area is an autumn breeder with larval hibernation.

Patrobus atrorufus. The species was caught from May to November with a maximum activity in July—September (Fig. 1). The annual activity rhythm thus resemble that of autumn breeders, and hibernation probably takes place in the larval stage, as in lower parts of central Norway (Refseth 1980), in Denmark (Jörum 1976) and in southern Europe (Thiele 1969).

Calathus micropterus. The species were found from May until November, with a maximum in the activity density in June and July (Fig. 1). This corresponds to the findings in Denmark (Larsson 1939). A small peak in activity density in September/October may indicate hatching in autumn as found in southern Sweden (Lindroth 1945), but the species is most probably an autumn breeder as described by Larsson (1939) in Denmark.

Calathus fuscipes (Goeze). Maximum activity density was found in July/August (Fig. 1), and animals were found from the beginning of April until the middle of September. This corresponds to findings in Denmark (Larsson 1939) and southern Sweden (Lindroth 1945), where the species is an autumn breeder with larval hibernation.

Carabus nemoralis Müller. The species was caught from April until November (Fig. 2). There was a rather high activity density during most of this period with a drop in June and November. Larvae were found during June and July. This corresponds to findings in Denmark (Larsson 1939) and in southern Sweden (Lindroth 1945) where the species is a spring breeder with adult hibernation.

Carabus problematicus Herbst. The species was caught from May until October. There was a top in the activity density in July/August, a drop in density in August/September and a little top in September/October (Fig. 2). Larvae were found from September until December. This correspond to findings in England (Houston 1981), where the species is a summer/autumn breeder with larval hibernation. My material also indicate summer dormancy as described by Drift (1959). In southern Sweden (Lindroth 1945) and Denmark (Larsson 1939) there is a top in activity density for this species in May and it is described as a spring breeder.

Carabus coriaceus (L.) Adults were caught from May until October, with maximum activity density in July/August. Larvae were found from April until July (Fig. 2). The species is probably an autumn breeder with larval hibernation. The annual activity densities correspond to the findings in southern Sweden (Lindroth 1945), but not to the findings in Denmark (Larsson 1939, Jörum 1976) where there was a low activity density in July and the maximum was found in September.

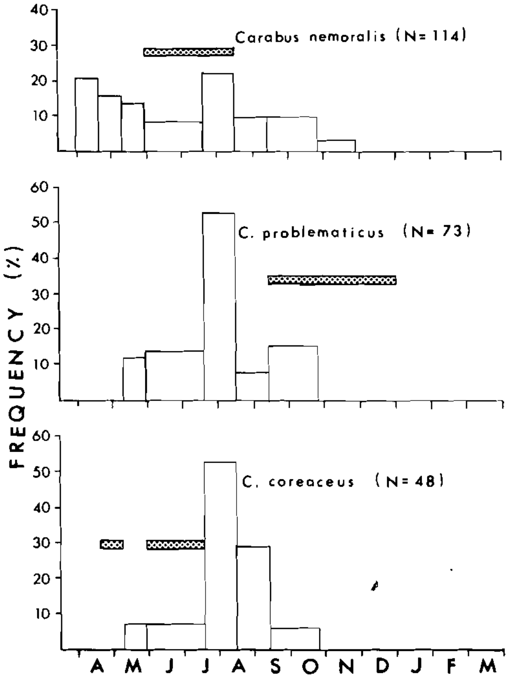

Fig. 2. Frequency diagrams of the trapping results of the *Carabus* spp. at Kålås. (Hatched area — larvae caught).

Pterostichus melanarius (Illiger). The species was caught from the end of April until the end of December with a top in activity density from June until the middle of August (Fig. 3). This top corresponds to findings in eastern Norway (Andersen 1982) but seems to be a little earlier than found in Denmark (Jörum 1976). The activity rhythm indicate that the species is an autumn breeder with larval hibernation (Larsson 1939, Lindroth 1945).

Pterostichus niger (Schaller). A marked top in activity density was found in July/August, and animals were caught from the middle of May to the end of October (Fig. 3). Lindroth (1945) found a top in activity density a little earlier in southern Sweden, but my findings correspond very well to Jörums (1976) findings in Denmark. The activity density resembles that of autumn breeders with mainly larval hibernation.

Pterostichus nigrita (Paykull). The species was only caught in April/May and in September/October

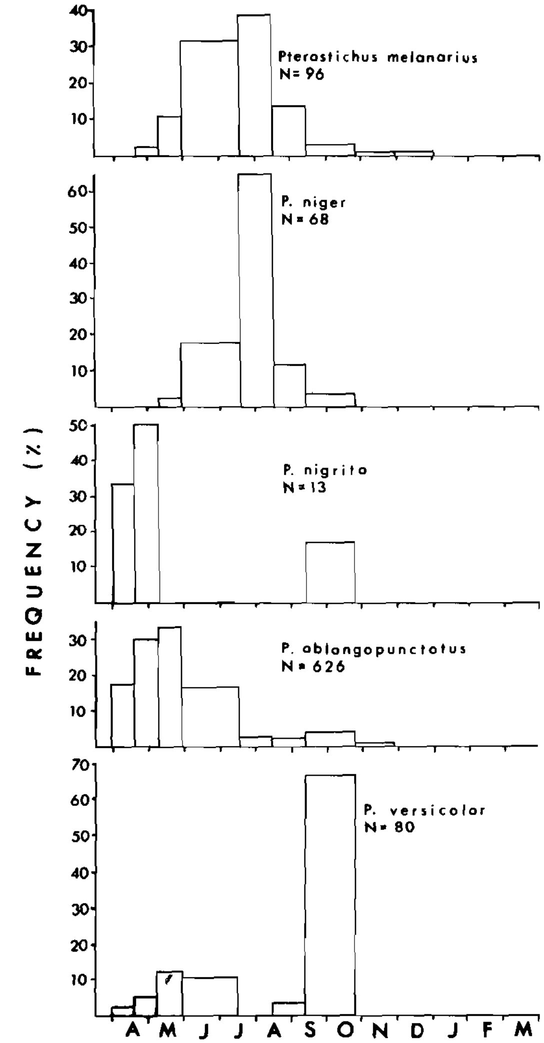

Fig. 3. Frequency diagrams of the trapping results of the *Pterostichus* spp. at Kålås.

(Fig. 3). This corresponds to findings in Denmark (Larsson 1939), but in southern Sweden there is a later top in spring activity and no top during the autumn (Lindroth 1945). Even if the sample is small (N = 13) it seems that the species is a spring breeder with adult hibernation.

Pterostichus oblongopunctatus. A top in activity density was found in April—June, and animals were caught from the beginning of April until the end of November (Fig. 3). The activity rhythm thus resemble that of spring breeders and hibernation probably take place in the adult stage, as found in Denmark (Larsson 1939), and southern Sweden (Lindroth 1945).

Pterostichus versicolor (Sturm). A peak in activity density was found in September/October and there was a smaller peak in May/June (Fig. 3). In Denmark (Larsson 1939) and in southern Sweden (Lindroth 1945) the activity density was greatest in May/June and there was only a small peak in the autumn. The autumn peak seems also to be a little later in my study area. The species is a spring breeder with adult hibernation.

CONCLUSION

The seasonal activity patterns found in this study correspond to a great extent to findings in Denmark (Larsson 1939, Jörum 1976) and southern Sweden (Lindroth 1945). Anyhow there are small differences observed for some species. Totally the material in this study seems to be more similar to the material from Denmark than to that from southern Sweden. One trend in the material, however, is that the autumn breeding comes a little earlier in my study area than in Denmark.

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Trapping efficiency of carabid beetles in glass and plastic pitfall traps containing different solutions

BJØRN ERLING WAAGE

Waage, B.E. 1985. Trapping efficiency of carabid beetles in glass and plastic pitfall traps containing different solutions. *Fauna norv. Ser. B. 32,* 33—36.

The trapping efficiency of Carabid beetles in glass and plastic traps containing 4% formol, soapwater, water and empty traps was tested. No differences were found in trapping efficiency between glass and plastic traps containing formol and soapwater. However, empty plastic traps had lower catches than empty glass traps.

A skeewed sex ratio in favour of females was found in empty plastic traps. Males in particular are suggested to escape more easily from plastic than from glass traps, which explains the differences in trapping efficiency observed.

No support was found of formol acting as an attractant.

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INTRODUCTION

Until the middle of the twentieth century the entomologists studying ground beetles went down on their knees with their pincers ready to attack every fleeing carabid that just had been deprived of its hiding place. This method, apart from it being very time-consuming, yields varying results according to the collector's searching image and endurance, thus making the method unsuitable for quantitative investigations.

The introduction of a pitfall trap (Barber 1931, cited in Southwood 1978) in the early 1930s formed the basis for the «evolution of pitfallogy». Since the mid-fifties a variety of modifications have been tested (Southwood 1978).

The method is passive and totally depends on the epigeous activity of different species. This activity is among other things modified by the habitat structure (Greenslade 1964) and the macro- and micro-climate (Briggs 1961, Desender & Maelfait 1983). The catches obtained by pitfall trapping do not necessarily give good estimates of the abundance of the different species, and therefore Heydemann (1953, cit. Thiele 1977) termed such estimates «activity density».

Many factors will influence the trapping results as reviewed in Adis (1979). One important factor is e.g. which material the traps are made of. Luff (1975) demonstrated that glass traps were more efficient than plastic traps. In his experiment the traps were all dry (empty). This is necessary in capture-mark-recapture investigations. But very often a preservative will be used, most frequently 4% formol (Skuhravy 1970). Formol traps often catch higher numbers of carabids compared to waterfilled traps, and the suggestion has been put forward that formol acts as an attractant (Luff 1968; Skuhravy 1970; Adis 1974, cit. Thiele 1977). The only direct observation of significant attraction has been reported in *Carabus problematicus* Herbst in June, and it did not remain constant during the year (Adis & Kramer 1975).

Luff (1975) found that empty glass traps were more efficient than plastic traps because of a higher retaining efficiency. These and similar results led Thiele (1977) to point out the toxicity of formaldehyde as an alternative explanation for the higher catches in formol traps.

In this experiment I primarily want to test the trapping efficiency of plastic traps as against glass traps when formol is used as killing-preserving agent, but in addition other contents as well as dry traps are tested.

STUDY AREA

The investigation was carried out in a small fallow field at Kistebakkane (60°23'N, 05°26'E) 17 km north of Bergen, western Norway. It was overgrown with *Rumex longifolius* L. and some *Ranunculus acris* L. The field was at the bottom of a southfacing slope covered with *Acer pseudoplatanus* L. and *Fraxinus exelsior* L.. The open areas east and south to the field were covered with grasses and are being harvested twice a year.

MATERIAL AND METHODS

Fifty pitfall traps, consisting of 25 straightsided glass jars (Ø 60 mm) and 25 plastic cups with slightly sloping sides (Ø 66 mm), were dug into the ground. They were arranged in five rows of ten traps each. Ten of each type of trap were kept empty, five were filled with water, five with water and soap, and five with 4% formol and soap. This made it possible to test the trapping efficiency both between glass and plastic traps and among traps of the same material with different content. The reason for using soapwater was that in the formol solutions one usually adds some soap to break the surface tension. This makes the insects drown more rapidly (Basedow 1976). The idea was that the soapwater traps would be intermediate between formol and water concerning retaining efficiency.

The distance between the traps were 1,5—2 m and no neighbour traps were of the same type. The traps were covered with roofs, made of galvanized iron sheet, which reached about 3 cm from the ground. The experiment was run for one week, July 13—21 1983. It was a rather rainy period (total amount of precipitation 61 mm, spread on 8 days; mean mean max./min. temp. 11.8°C), and 7 dry glass and 6 dry plastic traps were occasionally filled with rainwater.

RESULTS AND DISCUSSION

About 86% of the 233 specimens was made up of *Patrobus atrorufus* (67.4%) and *Trechus secalis* (19.3%), leaving 13.3% to the remaining species (Tab. 1). The total catches in the glass and plastic series (Tab. 1) were significantly different ($p < 0.001$). Although only 28% of the total catch were found in the plastic traps, more species were caught in these, though this difference is not statistically significant.

When glass and plastic traps with the same content were tested against each other (Tab. 2, 3), the differences were not significant in the formol and soapwater series. In the water and dry traps, on the other hand, the differences were highly significant ($p < 0.001$). Testing the glass series with each other gave no significant differences, whereas the tests yielded highly significant differences for the plastic series. If the sampling had been carried out using only plastic cups, one could have been tempted to conclude that this bias was due to formol acting as an attractant. The glass series shows that this is not the case. In fact, here the catches were higher in the water and dry traps. So at least in this investigation there seems to be no evidence in support of formol acting as an attractant.

The sex was determined, and the percentages of males are presented in Tab. 4. The X^2-test was applied to *P. atrorufus* since this was the only species caught in significant great numbers.

The glass series had approximately the same male percentages (56—65). In the plastic series this male dominance was only found in the formol traps. The difference between dry glass and plastic traps was highly significant.

Reduced catches in some of the plastic cups

Table 1. Number of species and specimens of different Carabid beetles caught in glass and plastic pitfall traps, Åsane, western Norway 1983.

Species	Glass (n = 25)	Plastic (n = 25)	Totals (n = 50)
Patrobus atrorufus (Strøm)	119	38	157
Trechus secalis (Paykull)	33	12	45
Pterostichus melanarius (Illiger)	7	2	9
P. niger (Schaller)	—	4	4
Clivina fossor (L.)	4	4	8
Nebria brevicollis (Fabricius)	2	—	2
Bembidion lampros (Herbst)	—	1	1
Leistus rufescens (Fabricius)	—	1	1
Harpalus affinis (Schrank)	1	—	1
Carabus hortensis L.	—	1	1
Amara aulica (Panzer)	—	1	1
A. spp.	1	2	3
Totals	167	66	233
Total no. of species	7	10(11)*	13(14)*

*A. spp. represents 2 or 3 species.

Table 2. Carabid beetles caught in glass and plastic pitfall traps with different solutions. n.s. = $p > 0.05$, + + + = $p < 0.001$ (X^2-tests, applied to no. of specimens).

	Glass Number of		Plastic Number of		Total Number of			
Traps	specimens	species	specimens	species	specimens	species	X^2	p
Formol and soap (n = 5) a)	30	3	25	7	55	7	0.46	n.s.
Water and soap (n = 5)	27	4	18	6	45	8	0.90	n.s.
Water (n = 5)	38	4	5	2	43	4	12.66	+ + +
Dry and rainwater (n = 10) b)	72(36)c)	6	18(9)c)	5	90(45)c)	8	16.20	+ + +
Totals	167	7	66	10	233	13(14)	21.89	+ + +
X^2 (p)	2.41 (n.s.)		16.75 (+ + +)					

a) No. of traps in each serie
b) Originally 10 dry traps in each serie were placed out, but 7 glass and 6 plastic traps were accidentally filled with rainwater
c) Expected no. of specimens caught in 5 traps

Table 3. Student-t test showing the significance in similarity of catches of *Patrobus atrorufus* in different trap types.

	Glass				Plastic			
	F	SW	W	DR	F	SW	W	DR
Glass:								
Formol (F)	—	n.s.	n.s.	n.s.	n.s.	n.s.	+	+
Soapwater (SW)	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	+
Water (W)	n.s.	n.s.	—	n.s.	n.s.	n.s.	+	+ +
Dry and rainwater (DR)	n.s.	n.s.	n.s.	—	n.s.	n.s.	+	+ +
Plastic:								
Formol	n.s.	n.s.	n.s.	n.s.	—	n.s.	+	+
Soapwater	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.
Water	+	+	+	+ +	+	n.s.	—	n.s.
Dry and rainwater	+	+	+	+ +	n.s.	n.s.	n.s.	—

n.s. = not significant): $p > 0.05$
+ = $p > 0.05$
+ + = $p > 0.01$

Table 4. Percent number of Males of Carabid beetles caught in pitfall traps with different solutions. Sample size as in tab. 2. The figures given in brackets are the values for *Patrobus atrorufus*. n.s. = $p > 0.05$, + + + = $p < 0.001$ (refers to *P. atrorufus*).

Traps	glass	plastic	totals	X^2	p
Formol and soap	53 (57)	48 (56)	51 (56)	0.26 (0.009)	n.s.
Water and soap	44 (58)	39 (46)	42 (53)	0.301 (1.385)	n.s.
Water	53 (56)	80 (50)a)	56 (56)		
Dry and rainwater	60 (65)	28 (22)	53 (68)	11.636 (21.253)	+ + +
Totals	55 (61)	42 (46)	51 (57)	1.742 (2.103)	n.s.
X^2	(0.848)	(14.771) b)			
p	n.s.	+ + +			

a) n = 2
b) water traps omitted (see a.)

may be caused by escape, as documented by Luff (1975). The distortion in sex ratio supports this, because male carabids are normally smaller and equipped with bristles on the anterior tarsals, facilitating climbing (Thiele 1977). Baars (1979) documents a higher escape of male *Calathus melanocephalus* L., which is about the same size as *P. atrorufus*. In the much lesser *Bembidion lampros* Herbst females escaped in higher numbers from glass traps containing 2% formol, but no escape was registered in middle-sized and large carabids (Petruska 1969).

To conclude, the plastic cups may be used when a 4% formol and soap solution acts as killing agent. When live catches are neccessary, glass traps will be more suitable.

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Larval morphology, habitat, and life cycle of the predaceous diving beetle *Laccophilus stroehmi* (Col., Dytiscidae)

GÖSTA HAGENLUND AND ANDERS N. NILSSON

Hagenlund, G. & Nilsson, A.N. 1985. Larval morphology, habitat, and life cycle of the predaceous diving beetle *Laccophilus stroehmi* (Col., Dytiscidae). *Fauna norv. Ser. B. 32,* 37-39.

The third instar larva of *Laccophilus stroehmi* Thomson is described from material from Sørlandet, Southern Norway. A key for the separation of the known third instar larvae of *Laccophilus* Leach is offered. The species is usually collected in oligotrophic lakes without fish. It is found at exposed shores on a sandy substrate with sparse vegetation. In Heilandsvann (Gjerstad, Aust-Agder) the life cycle is univoltine with larval development in the summer, mainly in July. The imagines overwinter in the lake.

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INTRODUCTION

Mainly due to its rareness, nothing has been known about the immature stages of *Laccophilus stroehmi* Thomson. In Fennoscandia this species is known only from very few localities, and in addition to some older records only single specimens have been found (Lindroth 1960. Strand 1970, Nilsson 1983). Fairly unexpectedly the species has recently been collected in high numbers in some lakes at Sørlandet, Southern Norway (leg. G. Hagenlund). Also larvae were found and it is now possible to give a description of the third-instar larva together with data on habitat and life cycle.

METHODS

Adults and larvae were collected with a sweepnet, used for one hour each sampling date. This way the relative abundance could be estimated. The collected material was preserved in ethanol. For the illustrations of the larva the relevant parts were mounted in Caedax on microscope slides. All measurements were taken with a micrometer eyepiece. The head length includes the neck and the width is measured across the eyes. The body length excludes the urogomphi.

As *L. stroehmi* was the only species of the genus at the intensively studied sites there can be no doubt on the identity of the larvae.

The preserved material is deposited at the Dept. Ecol. Zool., Univ. of Umeå, and in coll. Hagenlund, Oslo.

Laccophilus stroehmi Thomson, 1874. Figs. 1—4.

Diagnosis of larva: The larva of *L. stroehmi* is characterized by its dark colour that on the head forms a contrasty pattern. Head relatively narrow with about 6 posterior spine-like setae ventrally, clypeus with about 20 marginal lamelliform setae. Last abdominal segment broadly conical with a relatively short apical process, provided with a pair of long urogomphi each bearing about 20 longer and 20 spine-like setae. Legs long with swimming-hairs on all tibiae and tarsi and a relatively high number of spines.

Comparison with related species

In the European fauna *L. stroehmi* is most reminiscent of *L. minutus* (L.), a species that it at times has been mixed up with. The larva of *L. stroehmi* is very similar to that of *L. minutus,* of which the most detailed description was given by De Marzo (1976). Differences between these 2 larvae include the somewhat larger size and the darker tergal colour with a more contrasty patterned head of *L. stroehmi.* Also this species the last abdominal segment and the tarsi are provided with a somewhat higher number of spines. A valuable diagnostic character is the presence of 6—8 spine-like setae at the posterior half of the ventral side of the head in *L. stroehmi*. In *L. minutus* there are only 2 such setae.

Key

The third-instar larva of *L. stroehmi* is here included in the key presented by Nilsson (1982). This key is here slightly revised, and the original should be consulted for illustrations of the other species. The key now includes all Fennoscandian species of *Laccophilus*.

1. Last abdominal segment narrowly conical (length/width ratio about 2.5) with pointed apical precess and strongly pilose. Urogomphi shorter and with at most 20—25 setae each. Head short (length 1.00—1.10 mm)............................. *L. obsoletus* Westhoff
— Last abdominal segment broadly conical (length/width ratio less than 2.0) with apical process shorter and less pointed. Urogomphi longer and with at least 35—40 setae each. Head length exceeding 1.25 mm 2
2. Head narrow (length/width ratio 1.26—1.35). Clypeus anteriorly with about 20 marginal lamelliform setae. Length of last abdominal segment 0.88—0.94 mm 3
— Head broad (length/width ratio 1.12—1.22). Clypeus anteriorly with about 14 marginal lamelliform setae. Length of last abdominal segment 0.72—0.80 mm ... *L. hyalinus* (DeGeer)
3. Head ventrally with 6—8 spine-like setae in posterior half (Fig. 2). Body of a slightly darker tint and head with a more contrasty colour-pattern (Fig. 1)........... *L. stroehmi* Thomson
— Head ventrally with a single pair of spine-like setae in posterior half. Body of a lighter tint and head less contrasty patterned .. *L. minutus* (L.)

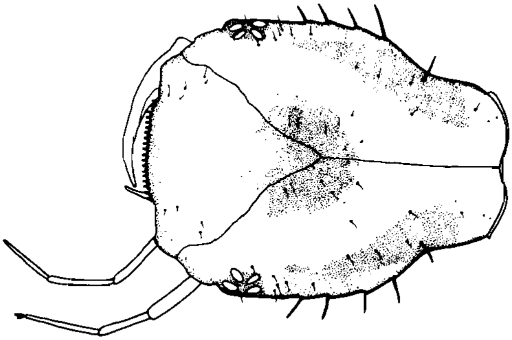
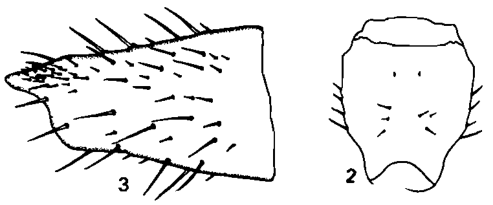


Fig. 1. *Laccophilus stroehmi*Thomson, head of third-instar larva, dorsal view.



Figs. 2—3. *Laccophilus stroehmi* Thomson, third-instar larva. —2. Head, ventral view. —3. Last abdominal segment, dorsolateral view.

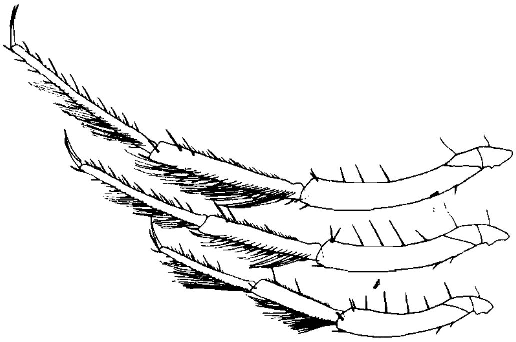


Fig. 4. *Laccophilus stroehmi* Thomson, right-side legs of third-instar larva, dorsal view.

Description

Colour. Head (Fig. 1) creamy yellow with distinct brownish median patch and posterolateral streaks; terga brownish yellow with pale lateral spots on the thoracic ones; legs and urogomphi pale.

Head (Figs. 1—2). Relatively narrow with sides subparallel; length 1.42—1.46 mm, width 1.10—1.14 mm; with 4—5 prominent temporal spines lypeus with about 20 marginal lamelliform setae; ventrally with 6—8 median spine-like setae in posterior half.

Legs (Fig. 4). Long and provided with swimming-hairs and a high number of spines; length of fore-tarsus 0.6 mm, of hind-tarsus 1.0 mm; hind- tarsus with about 14 ventral spines.

Body. Length about 4—6 mm, maximum width about 1.3 mm; last abdominal segment, (Fig. 3) 0.90 mm long broadly conical with relatively short apical process densely covered with long spines; length of urogomphi about 2.7 mm, each with about 20 setae and 20 spines.

Habitat

At Sørlandet, Southern Norway, the species has been found at varying densities in oligotrophic,

Table 1. Some chemical parameters of the lake Heilandsvann (Gjerstad, Aust-Agder) in Southern Norway in which *Laccophilus stroehmi* Thomson was frequently collected.

pH	4.8 ± 0.1	Ca^{++}	0.7 ± 0.2 mg/l
K_{18}	14 ± 2	SO_4^{--}	5.1 ± 1.7 mg/l
pT	7 ± 2	tot-Al	264 ± 74 µg/l

acid, clear water lakes, usually devoid of fish. The lakes are surrounded by coniferous forests (slowly growing *Pinus silvestris* L.).

The most intensively studied lake, Heilandsvann (Gjerstad, Aust-Agder), is situated 35 km from the coast at an altitude of 220 m aSL. The lake area is 7.2 ha and the amplitude is about half a meter. The littoral vegetation is dominated by *Lobelia dortmanna* L., *Juncus bulbosus* L. and *Carex rostrata* Stokes. In slightly deeper water there are water-lilies. The lake bottom consists of sand and rocks with a thin silt layer. Some chemical parameters are given in Tab. 1. These habitat characteristics are in good agreement with those given by Metsävainio (1922).

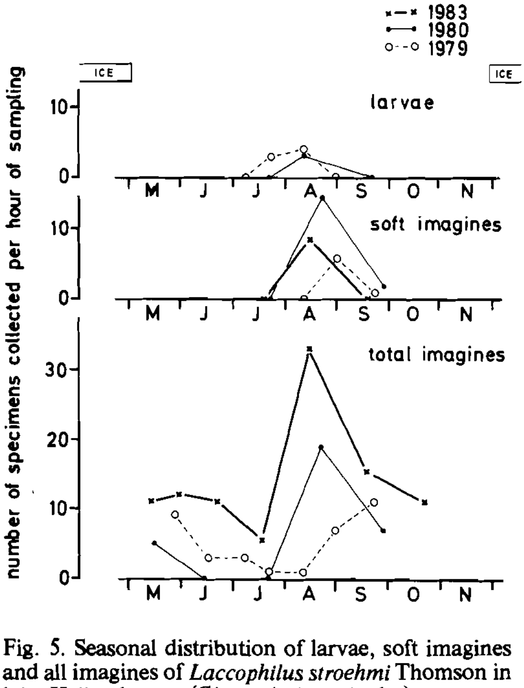


Fig. 5. Seasonal distribution of larvae, soft imagines and all imagines of *Laccophilus stroehmi* Thomson in lake Heilandsvann (Gjerstad, Aust-Agder).

The imagines were found swimming in the vegetation or above sandy bottom without a plant-cover. The larvae were closely associated with vegetation near the bottom.

Life cycle

The seasonal distribution of larvae and imagines is shown in Fig. 5. Mature imagines (recognized as females with mature eggs) were found in June. Third instar larvae were found in July and August. Soft imagines (newly emerged from pupae) appeared mainly in August, but some were collected also in July and September. The imagines overwinter in the lake, and mature the following spring. After the reproduction period the adult generation dies off during the summer. The life-span is thus about one year, though the possibility of occasional specimens living longer is not excluded.

A total number of 120 specimens were dissected. As the flight musculature was very poorly developed the species is seemingly flightless.

ACKNOWLEDGEMENT

We are most indebted to Dr. Luigi De Marzo of Bari, who kindly provided us with larvae for comparison.

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Nye funn av biller i Vestfold, Norge

BJØRNAR BORGERSEN, DAG EINAR HALVORSEN OG JAN ARNE STENLØKK

Borgersen, B., Halvorsen, D.E. & Stenløkk, J.A. 1985. New finds of Coleoptera in the province of Vestfold, Norway. *Fauna norv. Ser. B, 32,* 40—41.

36 species of Coleoptera are listed as new to the province of Vestfold. In addition, one specimen of *Eucnemis capucina* Ahrens (Eucnemidae), from Risør (AAy) is recorded for first time in Norway.

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NYE FUNN AV BILLER I VESTFOLD, NORGE

I denne listen rapporteres 36 nye funn av biller for Vestfold fylke, i henhold til Lindroth (1960) med senere korreksjoner. I tillegg er en art, *Eucnemis capucina* Ahrens (Eucnemidae), fra Risør (AAy) tatt med, da den ikke tidligere er kjent fra Norge.

Funnene er gjort i perioden 1977—1984, og oppbevares i samlingene til forfatterne (BB, DEH og JAS).

Nomenklaturen følger Silferberg (1979).

Karl Erik Zachariassen har vært behjelpelig med å bestemme enkelte funn.

CARABIDAE

Nebria livida (L.). VE: Tjølling, Hegdal, 15. aug. 1981. Et eksemplar på leirholdig bunn (DEH).

Stenolophus mixtus (Herbst). VE: Brunlanes, Kjose, 21. juni 1981. På sumpet ferskvannsbredd (DEH).

Calathus ambiguus (Paykull). VE: Tjølling, Hegdal, 12. april 1980 (2 eks.), samt 28. april 1980. Alle på nedlagt avfallsplass. (DEH).

Dromius schneideri (= marginellus) Crotch. VE: Larvik, 7. februar 1981. Under furubark (DEH).

CANTHARIDAE

Podaprus alpinus (Paykull). VE: Hedrum, Bjerke, 17. juni 1979. Slaghåv (BB). VE: Brunlanes, Pauler, 31. mai 1981, samt 24. juni 1982 (selje) (BB).

CLERIDAE

Tillus elongatus (L.). VE: Brunlanes, Kjose, 21. juni 1978. På gammel bjørkestokk (DEH).

Thanasimus femoralis (= rufipes) (Zetterstedt). VE: Brunlanes, Kjose, 4. april 1981. Under furubark (DEH).

MALACHIIDAE

Anthocomus bipunctatus Harrer. VE: Larvik, 9. juni 1980. Innenhus (BB). VE: Larvik, 16. juni 1981. Sittende på trafikkskilt (DEH), samt 18. april 1982, i flukt (DEH).

ELATERIDAE

Athous vittatus (Fabricius). VE: Tjølling, Heggedal, 29. mai 1981 3 eks. med slaghåv. (DEH). VE: Tjølling, Bisjord, 24. mai 1983. 4 eks. med slaghåv (BB).

Cidnopus (Limonius) pilosus (Leske). VE: Brunlanes, Pauler, 10. juni 1979. (JAS). VE: Tjølling, Heggedal, 28. mai 1982. 5 eks. på blomst av hegg (DEH), samt 2 eks. 29. mai 1982. VE: Brunlanes, 31. mai 1982. Funnet død i lite vann (BB).

Elater nigroflavus (Goese). VE: Brunlanes, Kjose, 3. mars 1981. I rødmuldrende stubbe (DEH). VE: Brunlanes, Pauler, 11. mai 1981. Flygende ved eik (BB).

Liotrichus (Corymbites) affinis (Paykull). VE: Brunlanes, Pauler, 18. juni 1980. Slaghåv (DEH). VE: Tjølling, Gon, 2. juli 1982. (BB). VE: Brunlanes, Kjose, 16. mai 1981. Slaghåv (DEH).

Orithales serraticornis (Paykull). VE: Brunlanes, Pauler. 2. juni 1981. På vedstabbel (BB).

Selatosomus (Corymbites) cruciatus (L.). VE: Brunlanes, 3. juni 1979. På ospestokk (DEH), samt 15. juni 1981 (BB).

Selatosomus (Corymbites) incanus (Gyllenhal). VE: Brunlanes, Kjose, 9. juli 1981. Banket av furu (DEH). VE: Brunlanes, Pauler, 29. mai 1982. På bjerk (BB).

BUPRESTIDAE

Agrillus biguttatus (Fabricius). VE: Brunlanes, Pauler, 11. juni 1980. Håv (BB). VE: Brunlanes, Kjose, 25. juni 1981. Flygende over blandingsved (DEH), samt 10. juli 1981 (DEH).

TROGOSITIDAE

Grynocharis oblonga (L.) VE: Brunlanes, Pauler, 30. mai 1982. Flygende (DEH).

ENDOMYCHIDAE

Mycetina cruciata (Schaller). VE: Brunlanes, Pauler, 26. juli 1981. Sittende på løvblad (DEH).

OEDEMERIDAE

Calopus serraticornis (L.) VE: Tjølling, Gon, 1. mai 1981. Tatt ved lys om kvelden (BB).

TENEBRIONIDAE

Prionychus ater (Fabricius). VE: Larvik. To larver funnet i hul, nedblåst alm 7. januar 1983, klekket i mai 1983, samt dødt eksemplar funnet på vei 18. juli 1983 (BB).

Opatrum riparium Scriba. VE: Tjølling, Vollen, 29. april 1984. Funnet på kirkegård (BB).

CERAMBYCIDAE

Tragosoma depsarium L. VE: Hedrum, Lauvevann, 6. aug. 1979. Sittende på tørt grantømmer (JAS).

Oxymirus (Toxotus) cursor (L.). VE: Brunlanes, Gui, 16. juni 1978. Krypende på bakken i hogstfelt (BB). VE: Tjølling, Heggedal, 18. juni 1978. Flygende (DEH). VE: Brunlanes, Pauler, 15. juni 1978. Flygende fra bøkeskog (BB). Andre fangstdatoer: 31. mai 1981 (4 eks. sittende på furubusk) (BB), 1. juni 1982 og 8. juni 1982 (Begge på blandingsved) (BB).

Anoplodera (Leptura) sexguttata (Fabricius). VE: Hedrum, Lauvesetra, 5. aug. 1979. På løvtreved (BB). VE: Brunlanes, Tvedalen (Mørje), 14. juni 1980 (JAS), samt 17. juli 1982 (BB). VE: Brunlanes, Pauler, 8. juni 1982. På eikeblad. (BB).

Judolia sexmaculata (L.). VE: Brunlanes, Dolven, 1. juni 1978. Slaghåv (BB). VE: Brunlanes, Pauler, 2. juli 1979. På løvtre (BB), samt 31. mai 1981, 8. juni 1982, 15. juni 1982 og 6. juli 1983. VE: Brunlanes, Sky, 3. juli 1980. Flygende (DEH). VE: Brunlanes, Kjose, 14. juni 1981. På granstokk (DEH). VE: Tjølling, Heggedal, 22. juni 1982. På ryllik (DEH). VE: Hedrum, Vestmarka, 6. juli 1982. På mjødurt (BB). VE: Hedrum, Bjerke, 7. juli 1982 (JAS).

Phymatodes alni (L.). VE: Brunlanes, Pauler, 19. juni 1977. 2 eks. på eikestokker (DEH), samt 10. juni 1979 (3 eks.) (DEH), 20. juni 1979 (4 eks.) (DEH), 31. mai 1984 (2 eks.) (BB). VE: Brunlanes, Tvedalen (Mørje), 24. juni 1980. (JAS), samt 2 eks. 31. mai 1984.

Pyrrhidium sanguineum (L.). VE: Brunlanes, Kjose, 10. mai 1981 (3 eks.), samt 12. mai 1981 (3 eks.). Alle på eik- og bjørkeved (DEH).

Semanotus undatus (L.). VE: Brunlanes, Kjose, 10. mai 1981 (3 eks.). Flygende (DEH). VE: Brunlanes, Pauler, 13. mai 1982. På furustokker (BB).

Pogonochaerus decoratus Fairmaire. VE: Tjølling, Sande, 8. juni 1979. Slaghåv (BB). VE: Hedrum, Bjerke, 25. juli 1979. På vedstabbel av blandingsved (BB). VE: Tjølling, Gon, 3. juni 1983. Slaghåv på eng (BB).

Pogonochaerus hispidulus (Piller & Mitterpacher). VE: Brunlanes, Paradiset, 22. mai 1977. Banket fra løvtre (DEH). VE: Brunlanes, Pauler, 10. juni 1979. På løvtømmer (BB), samt 19. juni 1979 (2 eks.) (DEH), 10. mai 1980, 9. juli 1980 og 2. juli 1980 (BB), og 9. juli 1980 (JAS).

Acanthoderes clavipes (Schrank). VE: Hedrum, Lauvevannet, 10. juli 1979. På blandingstømmer av løvtre (BB). VE: Brunlanes, Pauler, 18. juni 1980. 4 eks. på ospetømmer (DEH), samt 2 eks. 2. juli 1980 (JAS), 3. juli 1980 (BB), 2 eks. 27. juni 1982 (DEH) og 6. juli 1983 (BB). VE: Brunlanes, Kjose, 2. juli 1981. På ospetømmer (DEH). VE: Brunlanes, Tvedalen (Mørje), 5. juli 1982. Blandingstømmer (BB). VE: Brunlanes, Torpevannet, 5. august 1982. Blandinstømmer (BB).

Acanthocinus griseus (Fabricius). VE: Brunlanes, Tvedalen (Mørje), 19. august 1979 (JAS), samt 8. juli 1981 og 23. juni 1981 (BB).

Saperda perforata (Pallas). VE: Hedrum, Bjerke, 25. juli 1979. På vedstabbel av blandingsved (BB). VE: Hedrum, Lauvevannet, 5. aug. 1979 (JAS). VE: Brunlanes, Pauler, 26. juli 1981. På løvtrestokk. VE: Tjølling, Heggedal, 22. juni 1982. På vedstabbel.

ANTHRIBIDAE

Platyrrhinus resinosus (Scopoli). VE: Brunlanes, Pauler, 3. juli 1980. Tatt på vedstabbel (BB).

Platystomus (Anthribus) albinus (L.). VE: Hedrum, Bjerke, 3. juli 1979. På vedstabel av blandingsved (BB). VE: Brunlanes, Tvedalen, 5. juni 1980. På løvtre (BB). VE: Brunlanes, Pauler, 3. juli 1980 (JAS), 31. mai 1981, 15. juni 1981, 1. juni 1982, 24. juni 1982.

I tillegg til ovennevnte funn, har vi følgende art ny for Norge:

Eucnemis capucina Ahrens (Eucnemidae). AAy: Risør, 26. juli 1983 (BB).

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Interspecific association among millipeds from western and south-eastern Norway

ÅGE SIMONSEN

Simonsen, Åge. 1985. Interspecific association among millipeds from western and south-eastern Norway. *Fauna norv. Ser. B, 32,* 42—44.

Milliped species from western and south-eastern Norway are clustered using a Chi-square analysis of associations, and the coefficient of mean square contingency is calculated for all species pairs. The segregations among the species and the differences between the two areas are discussed.

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INTRODUCTION

A useful technique for identifying associations between species is to calculate coefficients based on the incidence of coexistence. It is a common observation that related species usually differ in their preferred habitats. At the extreme the segragation can be so complete that only one species of a taxonomic group inhabit a given habitat.

The present analysis attempts to identify milliped species associations in a multivariate way, so that clusters of associated species are identified.

The associations identified do not necessarily suggest causative relationships, but may instead relate to environmental factors controlling the distributions of the species. To test to which extend the millipeds are segregated by habitat preferances, two separate analyses have been carried out, one from the western and one from the south-eastern fauna. In this way associations due to similarities in the total distribution of the species are minimized and the associations will to a greater extend be due to similarities in habitat preferances.

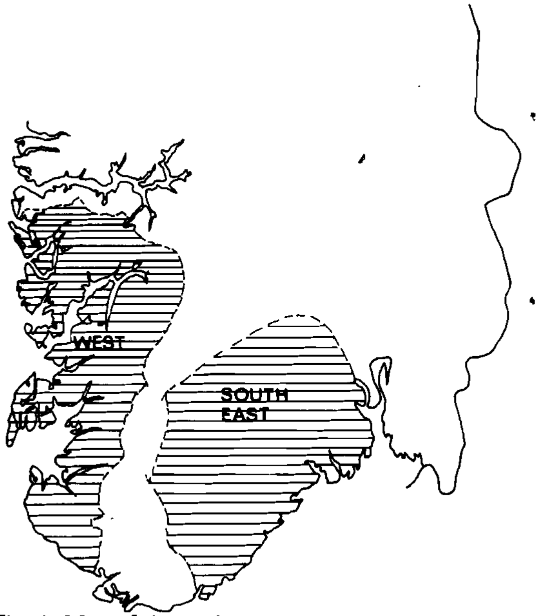

Fig. 1. Map of the study area.

THE STUDY AREAS

The sampling sites in the western area (Fig. 1) are mostly situated in mixed forests of decidous trees and pine. In this area the vegetation zones are boreo-nemoral or nemoral, a typical boreal zone is absent. The climate is humid and oceanic in the coastal areas and somewhat more continental in the innermost fjords.

In the south-eastern area (Fig. 1) there are three main regions: The oak-region of Southern Norway, The mixed forests-region and The premontane region. The vegetation zones are nemoral and boreo-nemoral in the oak and mixed forests regions and boreal in The premontane region. The climate is suboceanic in the coast areas and strong continental in the premontane region.

MATERIAL AND METODS

The present paper is based on millipeds collected in pit-fall traps from a total of 70 sites in the following provinces: Hordaland (4), Rogaland (21), Vest-Agder (13), Øst-Agder (5), Telemark (13), Vestfold (9) and Buskerud (5).

A 2 x 2 Chi-square test has been applied to calculate associations between the species.

$$X^2 = \frac{(ad - cd)^2 N}{(a + c)(b + d)(c + d)(a + b)}$$

where a = number of localities where both species were found together, d = number of localities where none of the species were taken, b and c = number of localities where only one of the species was found. A positive association exists when $(ad - cd) > 0$ and a negative association is found when $(ad - cd) < 0$.

$$C = \sqrt{\frac{X}{N + X^2}}$$ giving the association $-1 \leq C \leq 1$.

Two separate sets of analyses have been performed, one including the material from Øst-Agder, Telemark, Buskerud and Vestfold and one including the material from Rogaland and Hordaland.

As the 2 x 2 Chi-square test is a qualitative method testing for associations between species it should be applicable to pit-fall trap material.

A positive association between rare species might be obtained using the Chi-square test when including a high number of localities where the species are not taken. On the other hand, common species that are found together in all localities will show no positive association. These sources of error granted for, the method may provide adequate results.

RESULTS

Both in the western and the south-eastern area three main species association groups are established (Figs. 2, 3).

1. *Polydesmus denticulatus* (C.L. Koch 1887) groups with more synanthropic species.
2. *Proteroiulus fuscus* (Am Stein 1857) and *Polyxenus lagurus* (L. 1758) constitute a group in both areas. In the western area *Cylindroiulus punctatus* (Leach 1814) will group with these species, *Polydesmus denticulatus* takes its place in the south-eastern area.
3. In the south-eastern area is a noteworthly association between *Schizophyllum sabulosum* (L. 1758), *Cylindroiulus punctatus* and *Glomeris marginata* (Villers 1879).
   In the western area *Schizophyllum sabulosum* groups together with *Polydesmus, inconstans* Latzel 1884 and *Choneiulus palmatus* (Nemec 1855).

According to MacArthur, if the number of empty sites, i.e. those containing none of the species in a given group, exceeds expectation, then there must be some positive association and these may mask the effect of negative associations (if any) (MacArthur, 1972).

The test shows significant positive associations within all three species groups in the south-eastern area. Thus, these groups must be regarded as natural species groups. In the western area there is significant positive association within the group of synanthropic species only ($p < 0.02$), while the *Proteroiulus fuscus, Polyxenus lagurus* and *Cylindroiulus punctatus*-group shows a positive but not significant association. Within the group composed of *Schizophyllum sabulosum, Choneiulus palmatus* and *Polydesmus inconstans* the number of empty sites equals expectation, and the group may thus be artificial.

Two associations are similar in both areas: *P. fuscus* and *P. lagurus* show a positive association of 0.21 (N.S.) in the south-eastern area and 0.25 ($p < 0.05$) in the western one, and *P. denticulatus* and *Brachydesmus superus* Latzel 1884 show a positive association of 0.29 ($p < 0.05$) in the south-eastern area and 0.21 (N.S.) in the western one.

Proteroiulus fuscus shows a significant negative association both with *Polydesmus denticulatus* (-0.36, $p < 0.01$) and *Cylindroiulus punctatus* (-0.27, $p < 0.05$) in the south-eastern area, while in the western area these negative associations are not established. Furthermore, in the south-eastern area there is a significant positive association between *Choneiulus palmatus* and *B. superus* (0.36, $p < 0.05$), while in the western area the two species occur independent of each

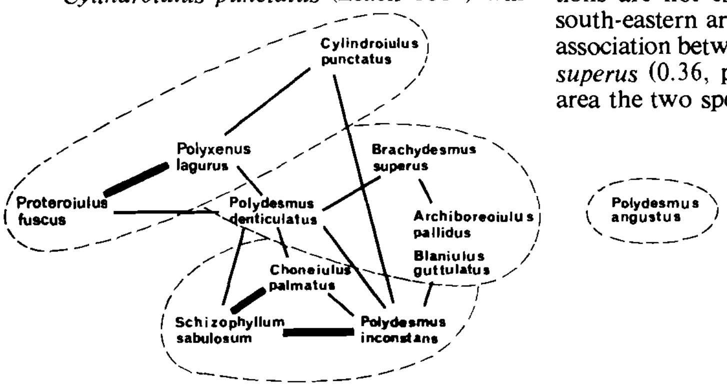

Fig. 2. Ordinated associations between the species in western Norway.
▬▬ significant positive association.
—— positive association.

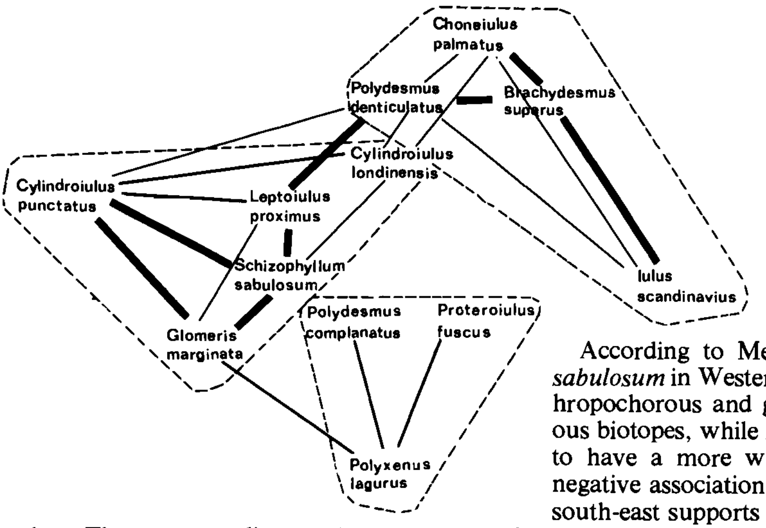

Fig. 3. Ordinated associations between the species in south-eastern Norway. ——— significant positive association. ——— positive association.

other. The same applies to *C. punctatus* and *Schizophyllum sabulosum* giving a positive association of 0.27 ($p < 0.05$) in south-east, but no association in the western area, and for *S. sabulosum* and *P. denticulatus* giving a negative association (− 0.32, $p < 0.02$) in the south-eastern area.

The differences found in species associations between the two areas are, however, in no cases so great that a positive association between two species is found in one area while a negative one is present in the other.

Two generalizations can be drown from the analysis:

1. Species belonging to the same genus are greatly segregated.
2. Species with same sort of life-histories occur significantly more often together than species with different life-histories, i.e. a semelparous species show greater association to other semelparous species than to iteroparous species and vica versa ($p < 0.001$).

DISCUSSION

For *Proteroiulus fuscus/Polydesmus denticulatus* and *P. fuscus/Cylindroiulus punctatus* the differences in associations between the two areas may be due to the fact that in most of the localities examined in Western Norway deciduous forest is dominating, the western parts of Norway offer no typical boreal zone. *P. fuscus* is common and often dominating in the boreal zone, while *P. denticulatus* seems to prefer calcareous coastal biotopes. The positive association between *Choneiulus palmatus,* which is concidered to be an anthropochorous species all over the country (Meidell 1972), and *Brachydesmus superus* in the south-eastern part of the country suggests that the latter species has a more anthropochorous distribution in this area.

According to Meidell (1972) *Schizophyllum sabulosum* in Western Norway appear to be anthropochorous and generally found on calcareous biotopes, while in Eastern Norway it seems to have a more widespread distribution. The negative association with *P. denticulatus* in the south-east supports this assumption.

Fairhurst and Armitage (1979) have grouped British millipeds together in a dendrogram of similarity of habitation sites. In this investigation *Cylindroiulus punctatus* and *Proteroiulus fuscus* group at approximately 80% likenéss. This is nicely in accordance with *C. punctatus* grouping with *P. fuscus* and *Polyxenus lagurus* in Western Norway.

Fairhurst and Armitage (1979) established great similarity in habitation sites for *B. superus* and *Polydesmus inconstans.*

Hauge et al. (1975) states that the two species is often found together in Western-Norway. However, the results from the western area indicate no such association.

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Short communications

LEPIDOSAPHES NEWSTEADI (SULC, 1895) (HOM., DIASPIDIDAE), A SCALE INSECT NEW TO NORWAY

D.J. WILLIAMS AND T. EDLAND

Lepidosaphes newsteadi (Sulc) has been found recently in Norway, the first record for Scandinavia and the most northerly record so far.

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The scale insect *Lepidosaphes newsteadi* has been collected recently in moderate numbers in Norway: Drøbak, on needles of *Pinus mugo* var. *mughus* (Scopoli) Zenari, 20 May 1984 *(T. Edland).* It has not been recorded by Kozarzhevskaya & Reitzel (1975) from Scandinavia nor by Danzig (1968) from northern Karelia. At latitude 59.40°N, Drøbak is the most northerly record so far. Elsewhere in Europe the scale insect is known from Czechoslovakia (type locality), France, Germany, Netherlands, Italy, Poland and Switzerland on *Pinus, Abies* and *Cedrus.* It has also been reported from Turkey on *Abies nordmanniana* subsp. *bornmuelleriana* and on *Pinus nigra* (identifications of the insect in need of confirmation) and from Lebanon on *Cedrus libani.*

Balachowsky (1954) has given good characters to separate *L. newsteadi* from *L. maskelli* (Cockerell) (now known as *L. pallida* (Maskell)). The most important character is the space between the median lobes. In *L. newsteadi* this space is always greater than the width of a median lobe, whereas in *L. pallida* the space is narrower. Furthermore, according to Balachowsky, in *L. pallida* there is always a single submarginal duct on the fifth segment and in *L. newsteadi* there are 4—6. In all the European material available of *L. newsteadi,* including original material sent by Sulc, there are only 2 submarginal ducts on the fifth segment.

L. newsteadi was reported from California and Mississippi in U.S.A. by Ferris (1937), but McKenzie (1956) has indicated that records from U.S.A. were based on misidentifications. Considerable damage by *L. newsteadi* on *Juniperus bermudiana* in Bermuda was reported in numerous articles during the 1940's and a history of the insect and attempts to control it were discussed by Thompson (1954). Many specimens are available, collected in Bermuda during the critical period, but an examination now shows that all are *L. pallida.* It seems certain therefore, that *L. newsteadi* is not present in the New World.

The biology of *L. newsteadi* has been discussed at some length by Mesnil (1949) who failed to find it on any species of *Juniperus* in Europe.

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EUPHRANTA (= RHACOCHLAENA) (LOEW, 1846) *(DIPT., TEPHRITIDAE)* NEW TO SCANDINAVIA

LITA GREVE AND ALF-JACOB NILSEN

Euphranta (= Rhacochlaena) toxoneura (Loew, 1846) is reported new to Scandinavia. One male was caught at Lomma, north of Malmö, Skåne province, Sweden, at 7 June 1961. Three males were caught in Malaise-traps, two males at Store Eikås, Gyland, Flekkefjord county, West Agder province, Norway, EIS 4, UTM 32 VLK 703724 between 21 June and 6 July 1982, the third male was caught at Sveindal, Laudal, Marnadal country, West-Agder province, EIS 5, between 21 July and 6 August 1982. The locality at Store Eikås was a wet meadow with both deciduous and coniferous trees, the locality at Sveindal a meadow in deciduous forest.

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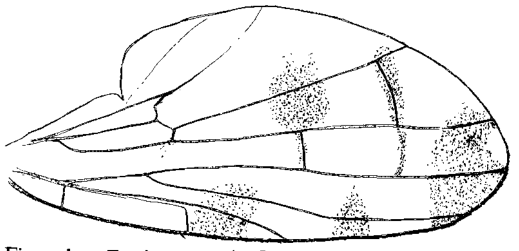

Fig. 1. *Euphranta (=Rhacochlaena) toxoneura* (Loew) Wing.

Euphranta (=Rhacochlaena) toxoneura (Loew, 1846) is the only species represented in Europe of the genus Euphranta. The generic name to use should be *Euphranta toxoneura* Loew, 1862 *(=Rhacochlaena toxoneura),* not *Euphranta (Staurella) toxoneura* Loew, 1862 as indicated by Hardy (1983), (Ian M. White pers.comm.).

The genus is represented in the Ethiophian region by several species. The species is not common in Europe. It has been recorded from Germany and Austria (Hendel, 1927), England (Kloet & Hincks, 1976) and Belgium (Seguy, 1934), but not from France (Seguy, 1934) or the Netherlands (Kabos, 1959). Neither the ecology (Hendel, 1927) nor the foodplants of the species are known (Niblett, 1955).

The only Swedish specimen in the collections of Lund University Museum is a male caught at Lomma, Skåne province at 7 June 1961. Dr. Hugo Andersson informed us of this specimen which he himself had collected and determined. Lomma is situated at the west coast of Skåne, slightly north of the city of Malmö.

Three male *E. toxoneura* were caught in Malaise-traps in West-Agder province, Norway, during the summer 1982. Two males were collected at Store Eikås, near Gausdal, Flekkefjord county, EIS 4, UTM: 32 VLK 703724 between 21 June and 6 July 1982. The locality was a wet meadow with both conifers and deciduous trees. The area must be described as boggy and small ponds were present. The third male was caught at Sveindal, Laudal, Marnardal county, EIS 5, between 21 July and 6 August 1982. The locality was a meadow with flowering plants in deciduous forest. The dominating species were *Cirsium heterophyllum L.* and *Chamaenerium angustifolium* (L.) Scop.

E. toxneura has not been recorded from Sweden (H. Andersson, pers. comm.). The species is not included in the last survey of the *Tephritidae* in Norway which is the more than a hundred year old list of Siebke (1877). *E. toxoneura* is, however, not represented in the collection of the Norwegian zoological museums in Oslo, Trondheim, Rana or Tromsø. Thus the four males mentioned here represent the first records for Scandinavia. *E. toxoneura* is not listed from Finland in Hackman's list from 1980.

The characteristic wing-pattern, shown in Fig. 1., should be sufficient to separate *E. toxoneura* from other Scandinavian *Tephritidae*. In specimens with damaged wings, the orbital bristles should be checked, the position of the orbital bristles are typical for the genus: The two lower pairs are placed closer together than the uppermost third pair. In addition the pair of inner vertical bristles are long and fairly strong. For a detailed description see Hendel (1927).

ACKNOWLEDGEMENTS

We are greatly indepted to Dr. Hugo Andersson, Lund for his permission to publish his specimen from Skåne as the first record from Sweden. We will also thank him for his information on the Swedish *Tephritidae* fauna. We will also like to extend our thanks to Dr. Brian R. Pitkin, British Museum (Nat.Hist.) for loan of material of *E. toxoneura* from England.

We are also thankful for the pers.comm. from Dr. Ian White on the generic name for *Euphranta (=Rhacochlaena) toxoneura* (Loew, 1846).

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A MASS OCCURRENCE OF *CYLINDROIULUS LONDINENSIS* (LEACH, 1815) IN NORWAY

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A mass occurrence of *Cylindroiulus londinensis* (Leach, 1815) took place in the Porsgrunn area, Norway, in late autumn 1980.

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INTRODUCTION

Mass occurrences of diplopods are rare in Northern Europe. The only comparable report is made by Lindgren (1942) from Sweden.

Normally mass occurrences of diplopods seems to consist of only one species, especially a iulomorph species.

In Norway *Cylindroiulus londinensis* (Leach, 1815) normally is found in low numbers at each locality. It seems distributed along the coast from Kristiansand in the south and to Oslo in the northeast. Two localities are found outside this area, one in the inner Hardangerfjord and one in the inner Sognefjord. This is a normal distributional pattern for diplopods entering Norway from the south-east (Meidell 1977, 1979).

The Porsgrunn area 1980

Porsgrunn lies in a calcareous area with rich vegetation. Reports of the mass occurrences in the autumn 1980 first reached us through the newspapers. Actually the people in the area were frightened by the wormlike animals that seemed to swarm out each evening, despite every effort of getting rid of them. Petroleum, brushes and spades had been tried, and thousands of animals were killed each night.

It was this problematic situation that made the newspaper contact us to hear if there was a more effective way of getting rid of these creatures.

MATERIAL AND METHODS

The area was investigated 3.—5. October. Unfortunately the number of animals had by then strongly decreased.

Samples made in the surrounding areas where the migrations started contained only 7 individuals pr. square metre, mostly juveniles. Two hundred and fiftysix individuals that had been killed earlier consisted of only adults. The following species were represented, the number of specimens indicated: *C. londinensis* (239), *Cylindroiulus punctatus* (Leach) (14), *Leptoiulus proximus* (Némec) (1) and *Choneiulus palmatus* (Némec) (2). Among the few animals sent to us by the newspaper was one specimen of *Unciger foetidus* (C.L. Koch), a species with a rather restricted distribution in Norway, previously known only from the Bergen area (Meidell 1968).

DISCUSSION

Trying to give explanations for mass occurrences and migrations of animals have always been a challenge to scientists. To be able to put forward at least a few hypotheses, some data on abiotic factors that could have influenced the diplopod populations in the area, have been collected. These are temperature, humidity and light. In both the best reported occasions, the animals were crawling on a white painted and diffusely illuminated brickwall. The animals were probably attracted to these areas and occurring on such white surfaces they were easily observed by people. Iulids are not normally observed climbing on such vertical walls as oniscoids, harwestmen and slugs are. Very little research has been done on positive phototactic reaction of millipeds.

The mass occurrences were reported during a period of decreasing temperature. Both for diplopods and other terrestrial invertebrates, it is known that the seasonal change in temperature might initiate movement or other activities. The mean temperature during the mass occurrences fell 3—4°C and passed 10°C. At the night between 4. and 5. October the animals ceased moving about when the temperature at the ground reached 5°C. The main problem is how could the population reach such a high number? No records of previous occurrences are made. The pattern in Porsgrunn, as well as in England (Blower 1969), seems to be that the young instars resides at their hatching site while only instar VI and VII are dispersing.

The previous years 1972—76 are characterized as abnormally dry, with the lowest precipitation for the season (April to August) recorded in 1976. The following years 1977—79 were abnormally wet. The resulting high production of vegetational material could have been the main factor behind the enormous number of animals that grew up in this area. The lifecycle of iulids should account for the fact that a growing population would be registered after two to three years, when the animals had reached the reproductive fase of their lives. There were signs of a similar mass occurrence in 1981. Now that contact is established with the local people we might be able to make a better investigation on this interesting phenomenon.

Compared with mass occurrences reported from tropical parts of the world, our might be classified as a minor one. It is often assumed that in the more temperate or colder climatic regions, the ecosystems are more simple. Whether this makes it easier to explain mass occurrences, remains to be seen.

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